Sexual Conflict in Orang-utans

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von

Julia Andrea Kunz

von

Brittnau AG

Promotionskommission

Prof. Dr. Carel P. van Schaik (Vorsitz & Leitung der Dissertation)

Prof. Dr. Wolf Blanckenhorn

Dr. Maria A. van Noordwijk

Dr. Tony Weingrill

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To my parents,

all the forests and its inhabitants

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Summary

Humans and orang-utans are the only primate species where forced copulations are frequently reported. In other primates, including African great apes, male aggression directed at females which qualifies as sexual coercion, is observed in more indirect forms, such as coercive mate guarding, intimidation, sequestration of females and infanticide. Sexual coercion as a research subject is sensitive and still elicits controversies, especially when suggesting an evolutionary approach to understand sexual coercion in humans. Yet, no work on nonhuman species can lead to a justification of human behaviour that has homologous or convergent manifestations in other species (anyone doing so commits the naturalistic fallacy). Evaluating biological explanations, however, will enable us to establish risk factors that make women vulnerable to coercion and eventually, to understand why sexual coercion is so frequent in human societies. In no other animal species, sexual coercion occurs in such abundance and diversity as in humans. The study of how and why sexual coercion has evolved in other species presents the opportunity to evaluate the biological basis of it objectively without a reporting bias.

Sexual coercion is the behavioural manifestation of sexual conflict: a conflict between the evolutionary interests of individuals of the two sexes in the mating context. Its common occurrence in many animal taxa suggests that it is not just a maladaptation, an evolutionary by-product or artefact, but that there is evolutionary continuity and hence, a biological explanation for sexual coercion. With this thesis, I set out to evaluate the occurrence of sexual coercion in orang-utans and bring it into the larger context of sexual conflict. There is high potential for the latter in orang-utans. First, they have an exceptionally slow life history with inter-birth intervals of 6 to 9 years resulting in a highly male-biased operational sex ratio (many sexually active males at the time, while only few females are ready to reproduce). Second, orang-utans are semi-solitary, and thus same-sex or opposite-sex protective associations are rare. Finally, there is a pronounced sexual dimorphism and females do not advertise fertility. Together, these factors make orang-utan females vulnerable to coercive males. Although forced copulations were largely labelled as a male reproductive strategy and hence, were associated with male quality and to some extent with female reproductive status, the females' fierce resistance to male mating initiations remained puzzling to researchers. Notably, forced and unforced copulations are sometimes observed even in the same male-female dyad within a few hours. Moreover, males appear to use just as much force as to overcome female resistance to achieve intromission and females have so far not been reported to incur any physical injuries resulting from forced copulations.

The semi-solitary lifestyle means that long-term data are essential to come to meaningful results. We evaluated long-term behavioural and endocrine data of two wild study populations – one at Suaq (10 years), Sumatra (*Pongo abelii*) and one at Tuanan (15 years), Borneo (*Pongo pygmaeus wurmbii*). The data showed that sexual coercion must not be regarded as a male strategy *per se*, but is the result of colliding male and female interests, i.e. a sexual conflict. Because males initiate most mating interactions, the leading question of this study was why and when females resist to male mating initiations and of course, when males mate and coerce. We evaluated the mating conflict in orang-utans on the level of individual males (second chapter – who coerces?) and females (fourth chapter – female sexuality), set it into the larger socio-ecological context (third chapter – cost of association) and finally, evaluated the immediate social context of sexual coercion (fifth chapter).

Orang-utan males show a unique bimaturism among primates and the two male morphs (unflanged and flanged) have been associated with alternative mating tactics. Flanged males exhibit fully developed secondary sexual characteristics, including cheek pads, increased body size, an enlarged laryngeal sac and emit loud calls (long calls), which mediate male competition and may attract fertile females. Unflanged males have not yet developed these SSCs and remain developmentally arrested, sometimes up to 20 years. Based on population averages, flanged males have generally been labelled as preferred by the females, and hence, were less frequently observed to force mating compared to unflanged males. However, geographic variation was reported in these behavioural patterns and generally ascribed to variation in the delay to the development of SSCs. Based on longitudinal data from

individual males who have transitioned from the unflanged to the flanged morph during the study period, we confirm the behavioural alternative reproductive tactics of the two morphs: Males associate and copulate more frequently in the unflanged morph than after developing into the flanged morph. Moreover, we show that sexual coercion is neither a male trait nor a morph-specific strategy of unflanged males, but rather a context-dependent tactic, which, however, ends up being more often used by unflanged males.

The absence of any morphological fertility advertisement by orang-utan females, as seen in the form of sexual swellings in many other old world primate species, is puzzling to researchers. In the third chapter of this thesis, we evaluated possible ecological explanations for this phenomenon. Sexual attractivity may be costly for females i) ecologically in terms of increased association frequency leading to feeding competition, and ii) because of increased male aggression rates. Female orang-utans incurred costs from increased scramble competition from both associations with males and females. Because the majority of associations with males were male-maintained and male-initiated, lasted longer than female-female associations and there was little evidence for social benefits to the females, we conclude that association maintenance is another context of sexual conflict in orang-utans. This conclusion is further supported by the increased female cortisol levels with increasing number of consecutive days in association with males. While males – especially those who cannot rely on female choice – need associations to mate and monitor female reproductive state and sexual activities, females incur costs from these associations, especially during lactational infertility. The most parsimonious explanation for the absence of fertility advertisements, which would concentrate male association and mating initiatives to certain time windows, is that female orang-utans trade-off the costs of association and the need for paternity confusion.

Male orang-utans appear to have very little information about a female's ovulatory state and accordingly associate and copulate during periods when females are highly unlikely to be fertile (chapter 4). We found that the onset of mating is often years prior to conception, which supports orang-utan females indeed have concealed ovulation. This finding strongly suggests that females benefit from confusing paternity. Thus, as in many other primate species, the risk of infanticide may select for unpredictable or even concealed ovulation, which enable orang-utan females to mate polyandrously, avoid monopolization by one (dominant) male, and thereby skew males' paternity assessment in their (infant's) interest. Although infanticide has never been directly observed in wild orang-utans and infant mortality is vanishingly small, the long inter-birth interval and slow reproduction rate of orang-utan females may make them very vulnerable to infanticide. Because orang-utan male dominance relationships fluctuate strongly and males often range widely with long absences from the study area over several months and up to years, females need an extended mating period to distribute paternity assessments efficiently. In sum, we show that female orang-utan mating patterns are consistent with female counterstrategies to infanticide.

Female resistance may add another layer to this paternity confusion strategy (chapter 5). Females could mate with the same male first and then strongly resist later. We therefore conclude that morph, male identity or male rank had no intrinsic effect on the likelihood of resistance. Instead, females were more likely to show resistance to copulations by males who were displaced in the course of the association. Thus, females resisted to mating initiations by males in the vicinity of more dominant males. Both the latency to the end of the association and the arrival of additional male associates was shorter when females resisted. On the one hand, subordinate males who are at the risk of displacement follow a *"now-or-never"* mating tactic, which translates into a *"best-of-a-bad-job"* strategy as they cannot rely on female choice. On the other hand, females appear to adopt a *"not-you-now"* resistance tactic, which leads to a skew in the paternity assessment of more dominant males, consistent with an infanticide avoidance strategy.

With this study, we uncovered a part of the larger socio-ecological context of mating conflict in orang-utans. We treated forced copulations as the result of the interaction between the interests of two players – male and female mating interests – and evaluated when these are at odds. Female mating strategies are consistent with infanticide avoidance, whereas both male coercion and competition appears to be driven by female preferences. Our study presents a starting point for detailed cross-species comparisons in the future to understand sexual coercion from an evolutionary perspective, and thus identify the particular risk factors from the female perspective.

Zusammenfassung

In der Ordnung der Primaten kommen erzwungene Paarungen nur in Orang-Utans und Menschen vor. In anderen Primatenarten, unter anderem auch den Afrikanischen Menschenaffen, tritt sexuelle Gewalt durch Männchen in indirekteren Formen auf, wie beispielsweise Zwangsbewachung von Weibchen (*mate guarding*), Einschüchterung, Segregation von Weibchen und Infantizid. Sexuelle Gewalt ist ein sensibles Forschungsgebiet und löst noch immer Kontroversen aus, vor allem in Betracht auf einen evolutionsbiologischen Ansatz um auch sexuelle Gewalt beim Menschen zu verstehen. Forschungsergebnisse von nichtmenschlichen Primaten, welche homologe oder konvergente Verhaltensweisen aufweisen, können keinesfalls zu einer Rechtfertigung von Menschenverhalten führen (jede/r die/der so etwas impliziert, begeht den naturalistischen Trugschluss). Die Auswertung von biologischen Erklärungen wird es jedoch ermöglichen Risikofaktoren, welche Personen für sexuelle Gewalt gefährdet sind, zu eruieren und letztendlich vielleicht helfen zu verstehen wieso sexuelle Gewalt so verbreitet ist in der menschlichen Gesellschaft. Bei keiner anderen Tierart tritt sexuelle Gewalt in solcher Vielfalt und Häufigkeit auf wie beim Menschen. Wann und in welchem evolutionären Kontext sexuelle Gewalt bei nichtmenschlichen Tierarten auftritt, erlaubt die objektive Evaluation einer biologischen Basis ohne Berichtsbefangenheiten.

Sexuelle Gewalt ist die Verhaltenserscheinung von sexuellem Konflikt: ein Konflikt zwischen den evolutionären Interessen von zwei biologisch verschiedengeschlechtlicher Individuen im Paarungskontext. Dessen verbreitetes Vorkommen im Tierreich suggeriert, dass es nicht nur eine Fehlanpassung, ein evolutionäres Nebenprodukt oder Artefakt ist, sondern dass es eine evolutionäre Kontinuität und deshalb auch eine biologische Erklärung für sexuelle Gewalt gibt. Mit dieser Dissertation, erforschten wir das Vorkommen von sexueller Gewalt in Orang-Utans (*Pongo spp*.) und brachten diese Verhaltensweise in den Kontext des sexuellen Konflikts. Das Potential für letzteres ist gross in Orang-Utans. Orang-Utans weisen eine sehr langsame *Life history* auf mit Zwischengeburtenintervallen von sechs bis neun Jahren, welche zu einem extrem hohen Männchen polarisierten operationalen Geschlechterverhältnis führt (viele reproduktionsbereite Männchen und nur wenig fruchtbare Weibchen). Zudem sind Orang-Utans grösstenteils einzelgängerisch, und damit sind beschützende gleich- oder andersgeschlechtliche Zusammenschlüsse rar. Dazu kommt der ausgeprägte Sexualdimorphismus und, dass Weibchen keine morphologischen Fertilitätsanzeichen aufweisen, wie andere Altweltaffen. All diese Faktoren zusammen führen dazu, dass das Potential für sexuelle Gewalt sehr hoch ist. Obwohl erzwungene Paarung ursprünglich als Fortpflanzungsstrategie von Männchen bezeichnet und somit mit der Männchenqualität assoziiert wurde und teilweise mit dem weiblichen Fortpflanzungsstatus, passte das Vorkommen dieser erzwungenen Paarung anhin in kein klares, evolutionsbiologisches Schema. Zum einen wurden erzwungene und einvernehmliche Paarungen in derselben Männchen-Weibchen Dyade innerhalb weniger Stunden beobachten. Zum anderen scheinen die Männchen gerade so viel Gewalt anzuwenden, um die Paarung zu erreichen – offensichtliche körperliche Verletzungen der Weibchen durch Gewalt von Männchen wurden bis anhin nicht beschrieben in Orang-Utans.

Die einzelgängerische Lebensweise der Orang-Utans machen Langzeitdaten unumgänglich für aussagekräftige Ergebnisse. Wir haben solche Langzeitverhaltens – und Hormondaten von zwei wildlebenden Studienpopulationen ausgewertet – Suaq (10 Jahre), Sumatra (*Pongo abelii*) und Tuanan (15 Jahre), Borneo (*Pongo pygmaeus wurmbii*). Unsere Daten zeigen, dass sexuelle Gewalt nicht einfach eine Männchenstrategie ist, sondern die Folge von divergenten Weibchen – und Männcheninteressen, also einem sexuellen Konflikt. Weil Männchen die meisten Verpaarungen initiieren, war die Leitfrage wann und wieso Weibchen sich diesen Paarungsanstössen widersetzten und wann Männchen sich verpaaren und Paarungen erzwingen. Wir haben den sexuellen Konflikt auf der individuellen Männchen- (zweites Kapitel – wer erzwingt?), und Weibchenebene ausgewertet (viertes Kapitel – weibliche Sexualität), haben den sozio-ökologischen Zusammenhang untersucht (drittes Kapitel –

Kosten von Zusammenschlüssen), und analysierten zuletzt die unmittelbaren sozialen Begebenheiten von sexueller Gewalt (fünftes Kapitel).

Orang-Utan Männchen weisen einen einzigarten Bimaturismus auf in der Primatenordnung und die zwei Männchenmorphe (unflanged und flanged) wurden durch alternative Reproduktionstaktiken charakterisiert. Backenwulstmännchen (flanged) weisen komplett entwickelte sekundäre sexuelle Charakteristiken (SSC) auf, unter anderem Backenwülste, erhöhte Körpergrösse, einen vergrösserten Kehlkopfsack und geben Rufe über grosse Distanzen (Long calls) ab, welche Männchen-Männchen Wettbewerb aushandeln und fortpflanzungsfähige Weibchen herbeiziehen. Männchen ohne Backenwülste (unflanged) weisen keine SSC auf und bleiben bis zu 20 Jahre entwicklungsgehemmt. Basierend auf Populationsdurchschnitten wurden Backenwulstmännchen (flanged) als von Weibchen bevorzugt beschrieben und folglich wurden erzwungene Verpaarungen häufiger von Nichtbackenwülstern (unflanged) beobachtet. Eine grosse geographische Variation in diesen Mustern herrscht jedoch vor, welche mit Unterschieden in der Entwicklungshemmung der SSC in Verbindung gebracht wurden. Unsere longitudinalen Daten von Männchen, welche die SSC während der Studienzeit entwickelt haben, bestätigen die alternativen Reproduktionstaktiken der beiden Männchenmorphe. Männchen verbringen mehr Zeit mit Weibchen und verpaaren sich häufiger während des unflanged Stadiums als nach der Entwicklung der SSC. Zudem zeigen wir, dass sexuelle Gewalt weder ein individuelles Merkmal von einzelnen Männchen noch eine morph-spezifische Verhaltensweise, aber stattdessen eine kontextabhängige Männchentaktik ist, welche jedoch vermehrt bei unflanged Männchen zum Zug kommt.

Dass Orang-Utan Weibchen ihre Fortpflanzungsfähigkeit nicht mit morphologischen Signalen anzeigen, wie andere Altweltaffen diese aufweisen (sexuelle Genitalschwellungen), ist ein Rätsel für die Wissenschaft. Im dritten Kapitel untersuchten wir mögliche ökologische Erklärungen für dieses Paradox. Sexuelle Attraktivität kann kostspielig sein für einzelgängerische Weibchen – zum einen wegen erhöhtem Futterwettbewerb durch vermehrte Zusammenschlüsse (*association*) mit Männchen und zum anderen durch erhöhte Aggressionsraten von Männchen. Es fielen ökologische Kosten an für weibliche Orang-Utans durch die erhöhte indirekte Konkurrenz (*scramble*) in der Nahrungssuche während Zusammenschlüssen mit anderen Männchen und Weibchen. Wir folgerten, dass solche soziale Zusammenschlüsse bei Orang-Utans ein weiterer Kontext von sexuellem Konflikt darstellt, weil diese grösstenteils von Männchen initiiert und beibehalten wurden und die Zusammenschlüsse mit Männchen von längerer Dauer waren als mit Weibchen und wenig Hinweise für soziale Vorzüge für Weibchen ergaben. Unser Fazit wurde von erhöhten Kortisolwerten von Weibchen, welche mehrere aufeinanderfolgende Tage mit Männchen verbracht hatten, gestützt. Während Männchen – vor allem diejenige, welche sich nicht auf Weibchenwahl verlassen können – Zusammenschlüsse mit Weibchen benötigen, um sich zu verpaaren und den Fortpflanzungsstatus und die sexuellen Aktivitäten von Weibchen zu beobachten, tragen die Weibchen die ökologischen Kosten dieser Zusammenschlüsse, vor allem während dem Zeitraum der Laktationsinfertilität. Die am besten unterstützte Erklärung für das Fehlen von morphologischen Fertilitätsanzeichen, welche das Männcheninteresse, inklusive die Zusammenschlüsse und Verpaarungsinitiativen, auf einen fixen Zeitraum legen würden, ist der Kompromiss zwischen den ökologischen Kosten für Zusammenschlüsse und der Notwendigkeit für Vaterschaftsverschleierung.

Orang-Utan Männchen scheinen sehr wenig verlässliche Informationen über den weiblichen Fortpflanzungsstatus zu haben und verpaaren sich demnach sogar, wenn Weibchen nicht fortpflanzungsfähig sind (Kapitel 4). Die Hypothese der verborgenen Ovulation in Orang-Utans wird durch unsere Beobachtungen, dass sich Weibchen bereits Jahre vor der Empfängnis verpaaren, unterstützt. Diese Erkenntnis unterstützt die Annahme, dass Weibchen Vaterschaftsverschleierung brauchen. Wie in anderen Primatenarten, selektiert das Infantizidrisiko folglich für unvorhersehbare oder sogar verborgene Ovulation, welche es den Orang-Utan Weibchen ermöglicht sich polyandrisch zu verpaaren und Monopolisierung durch ein dominantes Männchen zu umgehen und somit die

Vaterschaftswahrnehmungen der Männchen in ihren Interessen zu neigen. Obwohl Infantizid in wilden Orang-Utans nie direkt beobachtet wurde und die Säuglingssterblichkeit schwindend klein ist, könnten die langen Zwischengeburtenintervalle und die langsamen Reproduktionsraten Weibchen für Infantizid anfällig machen. Weil die Dominanzbeziehungen zwischen den Männchen stark fluktuieren können und Männchen oft über weite Gebiete streifen, mit langen Absenzen über mehrere Monate oder sogar Jahre vom Streifgebiet eines Weibchens, brauchen Weibchen eine stark verlängerte Paarungsperiode um Vaterschaftswahrnehmungen effizient zu verteilen. Schlussendlich zeigten wir, dass die Paarungsmuster der Weibchen kohärent sind mit einer Gegenstrategie zu Infantizid.

Das Resistenzverhalten der Weibchen scheint eine weitere Ebene zu dieser Vaterschaftsverschleierungstaktik hinzuzufügen (Kapitel 5). Weibchen verpaarten sich mit dem gleichen Männchen einvernehmlich und widersetzten sich später hartnäckig. Zusammen mit den vorhergenannten Ergebnissen folgern wir, dass weder Männchenmorph noch Qualität einen intrinsischen Effekt auf den Widerstand der Weibchen hat. Vielmehr widersetzten sich Weibchen eher den Paarungen von Männchen, welche durch ein anderes Männchen von der Proximität des Weibchens verscheucht (*displaced*) wurden während dem Zusammenschluss. Der Widerstand des Weibchens gegen Paarungsinitiationen trat also häufiger in der Nähe eines dominanten Männchens auf. Zudem endeten Zusammenschlüsse früher nach Paarungen mit Widerstand des Weibchens und andere Männchen näherten sich der Paarungsdyade mit kürzerer Latenzzeit als wenn die Paarung einvernehmlich war. Einerseits verfolgen untergeordnete Männchen, welche dem Verscheuchungsrisiko ausgesetzt sind, eine *"jetzt-oder-nie"* Paarungsstrategie, welche man zu einer "*best-of-a-bad-job*" Strategie übertragen kann, weil diese Männchen sich nicht auf die Weibchenwahl verlassen können. Die Weibchen, anderseits, scheinen eine *"nicht-du-jetzt"* Widerstandsstrategie zu betreiben, welche schlussendlich zu einer zu dominanten Männchen geneigten Vaterschaftswahrnehmung führt und somit mit einer Gegenstrategie zu Infantizid übereinstimmt.

Mit dieser Studie enthüllten wir einen Teil des grösseren sozio-ökologischen Kontextes des sexuellen Konflikts bei Orang-Utans. Wir haben das Vorkommen von erzwungenen Paarungen als Interaktionsergebnis von zwei Spielern – Männchen und Weibchen Interessen – behandelt und evaluiert, wenn diese nicht kompatibel sind. Die Paarungsstrategie der Weibchen sind vereinbar mit Infantizidverhinderung, während männliche Gewalt und Wettbewerb von Weibchenwahl geprägt wird. Unsere Studie präsentiert einen Ausgangspunkt für weitere, vergleichende Studien in der Zukunft um sexuelle Gewalt von einer evolutionsbiologischen Perspektive zu verstehen.

Ringkasan

Kejadian perkawinan paksa sering dilaporkan pada dua spesies primata, yaitu manusia dan orangutan. Pada jenis primata lain seperti kera besar Afrika, pemaksaan seksual oleh jantan lebih bersifat tidak langsung, misalkan penjagaan pasangan secara paksa, intimidasi, penarikan betina secara paksa , dan pembunuhan bayi. Topik pemaksaan seksual sebagai subjek penelitian merupakan topikyang sensitif dan masih memunculkan kontroversi, terutama ketika disarankan untuk digunakan sebagai sebuah pendekatan evolusi dalam memahami pemaksaan seksual pada manusia. Belum ada studi pada spesies bukan manusia (*nonhuman species*) yang dapat mengarah pada pembenaran perilaku manusia yang memiliki manifestasi secara homolog atau konvergen pada spesies lain (siapa pun yang melakukan hal tersebut melakukan kekeliruan naturalistik [*naturalistic fallacy*]). Namun, evaluasi terhadap penjelasan-penjelasan secara biologis akan memungkinkan kita untuk menetapkan faktor risiko yang mana perempuan rentan terhadap pemaksaan seksual, sehingga hal tersebut dapat digunakan dalam memahami penyebab pemaksaan seksual yang begitu sering terjadi pada masyarakat. Pemaksaan seksual jarang terjadi pada spesies lainnya, namun kejadian tersebut sering dialami oleh manusia. Studi tentang bagaimana dan mengapa paksaan seksual telah berevolusi pada spesies lain memberikan kesempatan untuk mengevaluasi dasar biologisnya secara objektif tanpa adanya bias dalam pelaporannya.

Pemaksaan seksual merupakan manifestasi perilaku dari konflik seksual, yaitu sebuah konflik evolusi dari dua individu berbeda jenis kelamin dalam konteks perkawinan. Hal ini sangat umum terjadi pada banyak spesies sehingga menunjukkan bahwa hal ini tidak hanya sekedar sebuah adaptasi/maladaptasi (sebuah produk samping dari evolusi), akan tetapi, ada kesinambungan evolusi sehingga diperlukan penjelasan secara biologis terkait pemaksaan seksual tersebut. Melalui disertasi ini, kami melakukan evaluasi terhadap terjadinya pemaksaan seksual pada orangutan dan sekaligus menjelaskannya dalam konteks konflik seksual yang lebih luas. Hal ini penting, mengingat adanya potensi yang tinggi akan punahnya orangutan. Pertama, orangutan memiliki jarak kelahiran yang sangat panjang dengan interval antar kelahiran antara 6 hingga 9 tahun sehingga menghasilkan adanya bias terhadap operasional rasio seks pada jantan (banyak jantan yang aktif secara seksual atau siap untuk kawin pada saat itu, tetapi hanya sedikit betina yang siap untuk bereproduksi). Kedua, orangutan bersifat semi-soliter, sehingga hubungan perlindungan antar sesama jenis atau lawan jenis jarang terjadi. Terakhir, ada dimorfisme atau perbedaan tanda seksual yang nyata antara jantan dan betina serta betina tidak menunjukkan tanda-tanda kesuburan. Faktor-faktor tersebut mendorong orangutan betina rentan terhadap terjadinya pemaksaan seksual yang dilakukan oleh orangutan jantan. Meskipun perkawinan paksa sebagian besar dianggap sebagai strategi reproduksi orangutan jantan, sehingga hal tersebut bisa dikaitkan dengan kualitas jantan dan kondisi status reproduksi betina, tetapi hal ini masih membingungkan para peneliti sehingga masih perlu diteliti lebih lanjut.

Mengingat orangutan merupakan hewan semi-soliter maka diperlukan koleksi data jangka panjang sehingga hasil yang dicapai akan lebih bermakna. Kami mengevaluasi data perilaku dan hormon dari dua populasi orangutan liar yaitu orangutan Sumatera (*Pongo abelii*) di Suaq Balimbing selama 10 tahun), dan orangutan Kalimantan (*Pongo pygmaeus wurmbii*) di Tuanan selama 15 tahun. Data menunjukkan bahwa pemaksaan seksual tidak bisa dianggap hanya sebagai strategi jantan untuk kawin, akan tetapi merupakan hasil dari adanya konflik kepentingan yang bersebrangan antara jantan dan betina yaitu konflik seksual. Oleh karena jantan umumnya yang menginisiasi atau mengawali sebagian besar interaksi perkawinan, maka pertanyaan utama pada penelitian ini adalah mengapa dan kapan betina menolak untuk kawin dan tentu saja ketika jantan kawin dan memaksa untuk kawin. Kami mengevaluasi konflik perkawinan pada orangutan pada tingkat individu jantan (bab kedua - siapa yang memaksa?) dan pada betina (bab keempat - seksualitas wanita), kemudian mengevalusinya ke dalam

konteks sosio-ekologis yang lebih luas (bab ketiga - biaya asosiasi) dan akhirnya, mengevaluasi konteks sosial langsung dari pemaksaan seksual tersebut (bab kelima).

Orangutan jantan menunjukkan karakteristik bimaturisme yang unik diantara primata yang mana ada dua bentuk morfologi jantan (jantan *unflanged* dan *flanged*) yang sering dikaitkan sebagai taktik kawin. Jantan berpipi besar (*flanged male*) menunjukkan bahwa karakteristik seksual sekunder (KSS) berkembang secara penuh meliputi bantalan pipi, peningkatan ukuran tubuh, pembesaran kantong tenggorokan, dan pengeluaran suara keras (suara panjang) yang memediasi kompetisi antar jantan serta dapat menarik betina yang sedang subur/fertil. Pada jantan berpipi kecil (*unflanged)*, KSS tersebut tidak berkembang dan perkembangannya kadang terhambat hingga 20 tahun. Berdasarkan penelitian pada rata-rata suatu populasi, jantan berpipi besar umumnya merupakan jantan yang lebih disukai oleh betina, oleh karena itu pada jantan berpipi besar jarang ditemukan adanya pemaksaan kawin dibandingan dengan jantan berpipi kecil (*unflanged)*. Namun, terdapat variasi geografis yang dilaporkan untuk pola-pola tersebut dan secara umum dianggap berasal dari variasi ketika terjadi keterlambatan pada perkembangan KSSs. Berdasarkan data yang sangat panjang dari jantan yang telah bertransisi dari *unflanged* menjadi *flanged* selama periode penelitian, kami berhasil mengkonfirmasi perilaku strategi reproduksi dari dua tipe jantan tersebut: jantan memiliki hubungan dan lebih sering kawin ketika masih berstatus sebagai jantan *unflanged* dibandingkan setelah berkembang menjadi jantan *flanged*. Selain itu, hasil penelitian menunjukkan bahwa pemaksaan seksual bukanlah merupakan sifat atau strategi khusus dari jantan *unflanged* tetapi lebih merupakan strategi yang bergantung pada konteks, dimana lebih sering digunakan oleh jantan *unflanged*.

Tidak adanya tanda kesuburan secara morfologis pada orangutan betina, seperti yang terlihat pada banyak spesies primata dunia lama lainnya, hal ini membingungkan bagi para peneliti. Pada bab ketiga dari disertasi ini, kami mengevaluasi kemungkinan adanya penjelasan secara ekologis untuk tidak adanya tanda kesuburan secara morfologis pada orangutan betina, seperti pembengkakan seksual. Daya tarik seksual sebagai tanda kesuburan bisa jadi justru membutuhkan biaya (*cost*) yang mahal bagi betina karena i) secara ekologis hal ini akan meningkatkan frekuensi terhadap adanya kompetisi pemberian makan; dan ii) terjadi peningkatan agresi antar jantan. Orangutan betina akan mengeluarkan biaya dari adanya peningkatan persaingan tersebut baik dengan jantan maupun betina lainnya. Karena sebagian besar hubungan dengan jantan akan dipelihara oleh jantan sekaligus diprakarsai oleh jantan, maka hubungan antara jantan-betina akan bertahan lebih lama dibandingkan hubungan antara betina-betina dan hanya ada sedikit bukti terkait dengan manfaat sosial bagi betina, sehingga kami menyimpulkan bahwa pemeliharaan hubungan adalah konteks lain dari konflik seksual pada orangutan. Kesimpulan ini juga didukung data terkait mengenai adanya peningkatan konsentrasi metabolit hormon kortisol pada betina ketika terjadi peningkatan jumlah hari dalam hubungan dengan jantan. Sementara pada jantan, terutama jantan yang tidak dapat bergantung pada betina yang dipilih, maka memerlukan adanya asosiasi untuk dapat kawin, pemantauan status reproduksi betina, dan kegiatan seksual betina, sehingga betina harus menanggung biaya dari hubungan ini, terutama selama periode infertilitas pada saat masa laktasi (menyusui). Inti penjelasan yang paling tepat terkait tidak adanya tanda kesuburan pada orangutan betina, yang akan menyebabkan jantan dapat menentukan waktu yang tepat dalam menentukan hubungan serta inisiatif untuk melakukan perkawinan pada waktu tertentu adalah agar biaya hubungan bisa dikurangi sekaligus untuk membingungkan jantan terkait induk jantan dari anak yang dilahirkan (*paternity confusion*).

Orangutan jantan tampaknya tidak banyak memiliki informasi tentang waktu ovulasi pada orangutan betina dan akibatnya, hubungan dan perkawinan terjadi selama periode ketika betina dalam keadaan tidak subur (Bab 4). Hasil penelitian ini menunjukkan bahwa awal perkawinan sering terjadi beberapa tahun sebelum kebuntingan (pembuahan), hal ini semakin menegaskan bahwa jantan tidak memiliki informasi mengenai status ovulasi betina (ovulasi tersembunyi). Hasil penelitian ini menunjukkan bahwa orangutan betina mendapatkan manfaat dari fenomena ini terutama untuk

membingungkan jantan terkait ayah dari anak yang dilahirkan. Dengan demikian, seperti halnya pada banyak spesies primata lainnya, maka risiko terjadinya pembunuhan bayi yang tidak dapat diprediksi dapat dihindari, sehingga akan memungkinkan orangutan betina untuk kawin dengan banyak jantan *(polyandrous),* menghindari monopolisasi oleh seekor jantan dominan, dan dengan demikian jantan-jantan lainnya akan cenderung menilai bahwa bayi tersebut adalah keturunannya. Meskipun pembunuhan bayi pada orangutan liar tidak pernah diamati secara langsung dan kematian bayi semakin kecil, panjangnya interval antar kelahiran dan lambatnya tingkat reproduksi pada betina dapat menyebabkan mereka sangat rentan mengalami kejadian pembunuhan bayi. Oleh karena hubungan dominasi orangutan jantan sangat berfluktuasi dan lamanya ketidakhadiran jantan-jantan di lokasi penelitian yaitu dari beberapa bulan hingga bertahun-tahun,maka orangutan betina memerlukan periode kawin yang panjang untuk mendistribusikan penilaian induk jantan secara efisien. Secara singkat, hasil penelitian ini menunjukkan bahwa pola perkawinan orangutan betina konsisten dengan strategi betina dalam melawan pembunuhan bayi.

Pada Bab 5, hasil penelitian menunjukkan bahwa resistensi betina ternyata merupakan bentuk lain dari strategi betina untuk membingungkan orangutan jantan. Betina dapat melakukan perkawinan terlebih dahulu dengan jantan yang sama, namun akan menolak jantan tersebut pada kesempatan lainnya. Oleh karena itu, dari penelitian ini dapat disimpulkan bahwa identitas jantan atau status dominasi jantan tidak memiliki pengaruh secara intrinsik terhadap kemungkinan resistensi orangutan betina tersebut. Sebaliknya, betina lebih cenderung menunjukkan resistensi terhadap perkawinan yang dilakukan oleh jantan selama periode menjalin hubungan. Dengan demikian, betina menolak perkawinan yang diinisiasi oleh jantan lainnya saat berada di sekitar jantan yang lebih dominan. Kondisi latensi hingga akhir hubungan dan kedatangan jantan lainnya akan berlangsung lebih singkat ketika betina malakukan penolakan. Di satu sisi, jantan bawahan (*subordinate*) memiliki risiko berat dalam melakukan taktik perkawinan yaitu, "sekarang atau tidak pernah" *(now-or-never)*, yang juga bisa diterjemahkan menjadi suatu strategi "melakukan hal terbaik dari suatu hal yang buruk" (*best-of-a-bad-job")* karena jantan bawahan tidak dapat berharap banyak untuk dipilih oleh betina. Di sisi lain, betina tampaknya mengadopsi taktik perlawanan yaitu "bukan kamu sekarang" *(not-you-now)*, yang mengarah pada kecenderungan jantan dominan dalam menilai siapa induk jantan dari anak yang dilahirkan dimana hal tersebut konsisten dengan strategi menghindari terjadinya pembunuhan bayi orangutan.

Dari penelitian ini, kami menemukan suatu bagian terkait konteks sosial-ekologis dari konflik perkawinan pada orangutan. Kami setuju bahwa perkawinan paksa merupakan suatu hasil dari adanya interaksi antara kepentingan dua pemain, yaitu kepentingan kawin antara jantan dan betina dan dievaluasi ketika hal tersebut bertentangan. Strategi kawin pada betina lebih konsisten dengan menghindari terjadinya pembunuhan bayi *(infanticide)*, sedangkan perkawinan paksa dan kompetisi antar jantan lebih didorong oleh preferensi atau tingkat kesukaan betina. Penelitian ini mempresentasikan suatu titik awal untuk perbandingan antar spesies secara terperinci di masa yang akan datang untuk memahami pemaksaan seksual dari perspektif evolusi dan mengidentifikasi faktor risiko tertentu dari perspektif betina.

Résumé

Humains et orang-outans sont les seules espèces de primates parmi lesquelles des accouplements forcés sont fréquemment signalés. Chez les autres primates, comprenant les grands singes africains, la coercition sexuelle exercée par les males sur les femelles est observée sous des formes plus indirectes comme le "mate guarding", l'intimidation, la séquestration ou encore l'infanticide. La coercition sexuelle est un sujet sensible en recherche et soulève généralement de nombreux débats, en particulier lorsqu'elle est étudiée dans une approche évolutive afin de mieux comprendre notre propre sexualité. Pourtant, aucune étude portant sur d'autres espèces ne peut permettre de justifier le comportement humain car il s'agirait alors d'un sophisme naturaliste. En revanche, cela peut aider à mieux déterminer les mécanismes biologiques qui régissent notre sexualité, identifier les facteurs rendant les femmes vulnérables à la coercition sexuelle et comprendre pourquoi ce phénomène est si présent chez l'être humain. En effet, aucune autre espèce animale ne montre une telle abondance ou diversité pour ce comportement sexuel particulier.

La coercition sexuelle est la manifestation comportementale du conflit sexuel : le conflit entre les intérêts évolutifs des deux sexes dans le contexte de reproduction. Sa présence apparue indépendamment chez de nombreux taxons démontre qu'il ne s'agit pas d'une mal adaptation isolée ou d'évènements anecdotiques mais au contraire, d'un résultat issu de mécanismes socio-écologiques complexes et sélectionné au cours de l'évolution des espèces. Dans cette thèse, nous avons étudié l'occurrence de la coercition sexuelle chez les orang-outans (*Pongo spp*.) afin de le replacer dans le contexte plus large du conflit sexuel, qui semble avoir un rôle important chez ces grands singes à cause de leur biologie particulière. Premièrement, ils possèdent un cycle de vie exceptionnellement lent avec des intervalles de 6 à 9 ans entre chaque grossesse avec un unique enfant, ce qui a pour cause un grand nombre de mâles sexuellement actifs pour très peu de femelles fertiles. Deuxièmement, les orang-outans sont semi-solitaires et s'associent rarement, il n'existe donc pas de coalition défensive, que ce soit entre membres du même sexe ou du sexe opposé. Troisièmement, le dimorphisme sexuel est prononcé avec une différence de taille importante en faveur des mâles et quatrièmement, les femelles n'avertissent pas de leur fertilité (au contraire de la plupart des autres espèces de primates). Ensemble, ces critères rendent les femelles vulnérables aux mâles coercitifs. Et en dépit du fait que l'accouplement forcé a été défini comme une stratégie des mâles, associée à leur "qualité" intrinsèque et d'une certaine manière au statut reproducteur des femelles, c'est un phénomène qui reste en grande partie incompris.

Le style de vie semi-solitaire des orang-outans a pour conséquence la nécessité de collecter des données sur le long terme afin d'obtenir des résultats significatifs. Nous avons donc utilisé des données comportementales et endocriniennes collectées sur deux populations sauvages – à Suaq, Sumatra sur 10 ans (*Pongo abelii*) et à Tuanan, Bornéo sur 15 ans (*Pongo pygmaeus wurmbii*). Les données suggèrent que la coercition sexuelle ne devrait pas être considérée comme une stratégie masculine *per se*, mais bien le résultat de la collision des intérêts mâles et femelles (i.e. conflit sexuel). Puisque les mâles initient la grande majorité des interactions sexuelles, les questions principales posées dans cette étude sont les suivantes : "Quand et pourquoi les femelles résistent-elles à un accouplement ? Quand les mâles tentent-ils de s'accoupler ou/et quand tentent-ils de forcer l'accouplement?". Nous avons évalué le conflit sexuel chez les orang-outans d'abord du point de vue des mâles (deuxième chapitre – quels sont ceux qui forcent ?) et des femelles (quatrième chapitre – sexualité des femelles). Nous avons redéfini de manière large le contexte socio-écologique chez les orang-outans (troisième chapitre – les coûts de l'association) et nous avons finalement évalué le contexte social immédiatement observé à l'instant où a lieu un accouplement forcé (cinquième chapitre).

Les mâles orang-outans possèdent deux formes matures différentes et les deux morphes (unflanged et flanged) ont été associés à des stratégies reproductives différentes. Les mâles "flanged" arborent des attributs sexuels secondaires entièrement développés comme des excroissances cutanées faciales, une taille corporelle augmentée, un sac gulaire permettant d'émettre des vocalisations longue portée qui sont utilisées à la fois pour la compétition entre mâles et pour attirer les femelles fertiles. Les

mâles “unflanged” n’ont aucune de ces caractéristiques secondaires et semblent être en arrêt développemental, parfois pendant plus de 20 ans. Les mâles “flanged” sont généralement considérés comme plus attractifs par les femelles et forcent moins fréquemment leurs accouplements comparés aux “unflanged”. Si l’on se base sur les données longitudinales des mâles étant passés de “unflanged” à “flanged” durant l’étude, nous confirmons les stratégies reproductives des deux morphes : les mâles s’associent et copulent plus avec des femelles lorsqu’ils sont “unflanged” que lorsqu’ils deviennent “flanged”. De plus, nous montrons que l’usage de coercition sexuelle n’est pas lié au mâle individuellement ni au morphe mais plutôt à une stratégie dépendante du contexte. Et celle-ci est largement plus utilisée par les “unflanged”.

L’absence de tout avertissement de fertilité des femelles, comme par exemple le gonflement des parties génitales observé chez de nombreuses autres espèces de primates de l’ancien monde, demeure curieuse pour les chercheurs. Dans le troisième chapitre de cette thèse, nous évaluons les potentielles explications biologiques responsables de ce phénomène. Dans le cas des orang-outans femelles, être attractives sexuellement peut être couteux i) écologiquement parlant si cela augmente trop fortement la fréquence d’association avec les mâles créant ainsi une compétition accrue pour la nourriture ; et ii) à cause d’une augmentation des agressions provenant de ces mâles. Pour les femelles orang-outans, toute association est couteuse que ce soit avec un mâle ou une autre femelle, en particulier lorsqu’elles sont toujours en période d’allaitement. Dans le cas des associations femelle-mâle, elles sont en majorité initiées et maintenues par ces derniers en plus de durer significativement plus longtemps que les associations femelle-femelle. L’absence de bénéfice pour les femelles lors de telles interactions avec les mâles nous permet de conclure que le maintien de ces associations est un autre contexte de conflit sexuel chez les orang-outans. Cette conclusion est renforcée par les niveaux de cortisol relevés chez les femelles, qui augmentent avec le nombre de jours consécutifs en association avec des mâles. Les mâles, en particulier les moins dominants, ont au contraire besoin de s’associer le plus possible afin de s’accoupler et de surveiller l’état reproductif et les activités sexuelles des femelles avec d’autres mâles. Notre explication la plus parcimonieuse pour cette absence d’avertissement de la fertilité serait donc un compromis entre les coûts d’association et une stratégie de confusion de paternité pour limiter les risques d’infanticide.

Les mâles orang-outans semblent n’avoir que très peu d’informations sur le statu ovulatoire des femelles et de fait, s’associent et s’accouplent alors que les chances de fertilisation sont parfois nulles (chapitre 4). Pour chaque femelle, nous observons souvent des premiers accouplements plusieurs années Prior à une nouvelle naissance ce qui semble confirmer l’hypothèse d’une ovulation dissimulée. Cette découverte suggère fortement une stratégie de confusion de paternité. Comme chez d’autres espèces de primates, le risque d’infanticide peut conduire à une ovulation aléatoire ou même entièrement indécelable permettant aux femelles d’être polyandres, d’éviter la monopolisation sexuelle par un seul mâle dominant et donc fausser la perception des mâles environnants dans l’évaluation de leurs propres chances de paternité. Comme les relations de dominance entre les mâles orang-outans fluctuent grandement et que certains individus se déplacent sur de longues distances, pouvant parfois être absent de la zone d’étude pendant des mois ou années, les femelles ont besoin d’une période sexuelle active (mais non fertile) étendue afin de distribuer une fausse impression de paternité chez tous les mâles de manière efficace. Bien qu’aucun infanticide n’ait encore jamais été observé dans la nature chez les orang-outans et que la mortalité infantile soit extrêmement faible, l’intervalle de temps entre deux naissances est si important que la perte d’un enfant représenterait un coût énorme pour la femelle. Ceci peut expliquer la sélection de telles stratégies afin de contrer tout possibilité d’infanticide. En somme, la sexualité des femelles orang-outans semble être modelée par leur vulnérabilité aux infanticides et donc adaptée à une stratégie efficace de confusion de paternité contrant au mieux ces risques.

Nous montrons que la résistance des femelles pourrait venir renforcer cette stratégie de confusion de paternité (chapitre 5). En théorie, les femelles pourraient s’accoupler avec un seul mâle et résister à toute tentative provenant des suivants. Ceci n’étant pas le cas, nous concluons donc que le morphe, l’identité ou le rang des mâles n’a aucun effet intrinsèque sur la probabilité d’être résisté par

une femelle lors d'une interaction sexuelle. Néanmoins, la probabilité qu'une femelle résiste à un mâle est plus grande si celui-ci s'est fait bouter hors de proximité par un autre mâle à un moment donné de l'association. De plus, les femelles résistent davantage à un mâle si un autre, plus dominant, est dans les environs. En moyenne, pour les accouplements résistés observés, le délai avant la fin de l'association en cours et celui avant l'arrivée d'un autre mâle sont tous les deux significativement plus cours que dans les cas où il n'y a pas eu de résistance. Les mâles subordonnés qui encourent le risque d'être chassés par un autre mâle plus compétitif suivent une stratégie reproductive « maintenant ou jamais ». Les femelles, quant à elle, répondent par une stratégie reproductive de résistance « pas toi maintenant », faussant ainsi la perception des mâles plus dominants aux alentours. Cela correspondrait toujours à une tactique de confusion de paternité, créant en même temps une compétition parmi les membres du sexe opposé.

Avec cette étude, nous dévoilons une partie du large contexte socio-écologique qui régit le conflit sexuel chez les orang-outans. Nous traitons la coercition sexuelle comme le résultat de l'interaction entre les intérêts des deux sexes et évaluons à quels moments ces intérêts s'opposent. Les stratégies reproductives des femelles sont en accord avec une tactique d'évitement d'infanticide tandis que celles des mâles semblent orientées par la compétition instillée par le choix des femelles. Notre étude constitue un premier pas vers une plus large comparaison inter-espèces dans le futur afin de comprendre la coercition sexuelle d'un point de vue évolutif et d'identifier les facteurs qui rendent les femelles de certaines espèces vulnérables.

Chapter 1: General Introduction – Sexual Conflict in Orang-utans

Orang-utans are the only non-human primate species where forced copulations are relatively frequently reported. Forced copulations in orang-utans were commonly regarded as a *"best-of-a-bad-job"* strategy of non-preferred males. However, sexual interactions themselves appear highly ambiguous in orang-utans: indeed, forced and unforced copulations were sometimes observed in the same dyad within a few hours (Knott, 2009). Moreover, males rarely inflict physical injuries to females, but appear to use as much force as to achieve copulation (ibid.). With some exceptions (Fox, 1998; Knott et al., 2010), research on the proximate mechanisms and ultimate causes of sexual coercion in orang-utans has long been limited to documenting it: quantifying its occurrence and characterising coercive males. Forced copulation, as a form of sexual coercion, is the direct behavioural evidence for sexual conflict over mating, and thus, a behaviour shaped by sexual selection.

Sexual selection theory

Sexual selection theory is based on males and females having different reproductive optima (Darwin, 1871). Females invest into quality (starting with few, large gametes) while males tend to invest into quantity (many small gametes) (Bateman, 1948). Besides the investment into larger gametes, females have potentially long periods of reproductive time out, during the period of gestation and lactation (in mammals), when they are not ready to reproduce. In contrast, males' reproductive time out after mating is generally short (van Schaik, 2016). This sex difference reflects that fact that females provide the majority of parental care, while males often contribute little direct infant care (Trivers, 1972). Accordingly, females are limited in their reproductive success by the access to resources, while males are limited by the access to mates (Emlen and Oring, 1977). This difference between males and females leads to high male-biased operational sex ratios, which may result in male-male competition (intra-sexual selection), female choice (inter-sexual selection) (Darwin, 1871) and sexual conflict (Parker, 1979). The three mechanisms of sexual selection, however, are not mutually exclusive and may be difficult to disentangle (Arnqvist and Rowe, 2005). One example illustrating the overlap are male secondary sexual characteristics. Ornaments may either signal fertility to females (female choice) or function as badges of status in male-male competition (Lüpold et al., 2019), while weapons, such as increased canine or body size, may serve either male-male competition or to overcome female resistance during mating interactions, i.e. in a sexual conflict context (Pradhan and van Schaik, 2009).

Pre- and post-copulatory processes of sexual selection

Sexual selection can manifest in pre- and post-copulatory processes. Darwin (1871) developed sexual selection theory based on his observations of pre-copulatory processes (e.g. the peacock's tail) and the majority of research effort since has focused on such mechanisms. Pre-copulatory processes of sexual selection are more readily identifiable: ornaments to display intrinsic viability to females (e.g. peacock's tail, birds of paradise), overt male-male competition such as physical fights (e.g. red deer or elephant seals), or the occurrence of forced copulations (a form of sexual conflict, see below). Only about a century post-Darwin, the importance of post-copulatory mechanisms was revealed (for reviews: Dixson, 2018; Eberhard, 2009), including sperm competition (Parker, 1970) and female cryptic choice (Thornhill, 1983), which may prompt sexually antagonistic coevolution (Arnqvist and Rowe, 2005) resulting in a sort of chemical warfare (e.g. seminal fluid and acidic vaginal tract in drosophila: Holland and Rice, 1999). Because research on post-copulatory mechanisms is often invasive, it is biased towards invertebrate species, where they were also first discovered. Likewise, sperm competition has been investigated quite intensively in insects, but also in other taxa, in which relative testis size was often used as a proxy for the sperm competition potential (short review: Harcourt, 1997; primates: Møller, 1988). Sperm competition and female cryptic choice occur (obviously) in species where females mate with multiple males when receptive (primates: Dixson, 2018) and therefore pre- and post-copulatory mechanisms are tightly interlinked (review for primates: Stumpf et al., 2011). Modelling approaches predict a trade-off between the investment into either pre- or post-copulatory sexual traits (Parker et al., 2013). In a comparative study on several vertebrate and invertebrate taxa, Lüpold and colleagues (2014) found that in species with low female monopolization potential prior to mating, the importance of post-copulatory relative to pre-copulatory sexual traits increases. Thus, even if there is evidence for male-male competition and female choice (pre-copulatory), post-copulatory processes may play an important role. In primates, relative testes size, as an indirect measure for the extent of sperm competition, was found to increase with male weapons (canine size), but to decrease with male ornaments (Lüpold et al., 2019). Although it remains difficult to directly assess the relative importance of pre-and post-copulatory mechanisms, there is ample evidence for post-copulatory processes acting in anthropoid primates (Dixson, 2018). We focus on pre-copulatory processes throughout this thesis. However, it needs to be kept in mind that there is room for post-copulatory mechanisms, and they likely shape primate sexuality.

Sexual conflict

Parker (1979) defined sexual conflict as 'a conflict between the evolutionary interests of individuals of the two sexes'. Anisogamy and asymmetrical parental investment set the scene for incompatible male and female reproductive optima (Parker, 1979; Trivers, 1972). Sexual conflict may arise in many contexts such as mate choice, mating rate and parental investment. Sexual conflict theory predicts an evolutionary arms race between the sexes: One sex attempts to shift the other's reproductive optimum towards its own and vice versa (Parker, 2006, 1979; Kokko and Jennions, 2008). Sexual conflict theory caused a paradigm shift from labelling mating or reproduction in general as a "benign endeavour" to a sexually antagonistic scenario with both females and males having opposing interests (Kokko et al., 2003; Tregenza et al., 2006). Studies on invertebrate species predominate the young field of sexual conflict: Fitness yields of both males and females can be measured and linked to behavioural and chemical evidence for sexually antagonistic coevolution (Arnqvist and Rowe, 2005; e.g. Mühlhäuser and Blanckenhorn, 2004). To study sexual conflict in animals with slow life history and more complex social systems and relationships is more challenging, because long-term data are needed to gain meaningful insights both concerning the proximate and ultimate causes (reviewed in Stumpf et al., 2011). Since sexual conflict has been defined as such (Parker, 1979), many different conceptual frameworks and definitions have been used and the concept remains hotly debated and difficult to grasp (Tregenza et al., 2006). Yet, sexual conflict both over mating and parental investment is expected to be

pronounced especially in those taxa with slow reproduction, such as mammals and particularly primates, where females have potentially long reproductive time outs and the operational sex ratio is highly male-biased. However, especially in those species *"it is extremely difficult to prove that sexual conflict occurs … because of the difficulty of measuring costs and benefits"* (Parker, 1979). We study one of those very slow species, orang-utans, and accordingly, the focus of the empirical study is on behavioural indicators of sexual conflict (mating and association maintenance). Nevertheless, these behavioural indicators provide hints towards colliding male and female interests, also from an ultimate perspective, such as the risk of infanticide and thus, paternity allocation (van Schaik et al., 2004).

Infanticide

Infanticide is an expression of a sexually selected male strategy (Hrdy, 1979; van Schaik and Janson, 2000) and thus, is an aspect of sexual conflict. Killing infants is adaptive for males, if i) the male is unlikely to kill his own progeny, ii) females return to fertility faster after losing a dependent infant than when weaning it and, iii) infanticidal males can ensure subsequent mating access to the female and thus, are likely the sire of the female's next offspring (Hrdy, 1979; van Schaik, 2000). Accordingly, infanticide is only an adaptive male sexually selected strategy when the lactation to gestation ratio exceeds 1, which is mostly found in toothed whales (*Odontoceti*), carnivores (*Fissipedia*) and primates (*Primates*) (to a lesser extent in rodents [*Scuriognathi*] and ungulates [*Perissodactyla*]) (van Schaik, 2000). In all of these taxa, infanticide by males has been reported (van Schaik, 2000). The majority of observed cases of infanticide are concentrated on periods after a change in male dominance hierarchy, especially when the new dominant male(s) has/have recently immigrated to the group and thus, no mating history with the local females (point i) above) (reviewed in Palombit, 2015; Hanuman langurs: Hrdy, 1974; long-tailed macaques: van Noordwijk and van Schaik, 2001; savannah baboons: Zipple et al., 2017).

Because infant loss imposes especially high fitness costs to females (and the male sire) in species with slow life history and low reproductive rates, various social and sexual counterstrategies to male infanticide have evolved (Clarke et al., 2009; Palombit, 2000, 2015; van Noordwijk and van Schaik, 2000; van Schaik et al., 2000; van Schaik and Kappeler, 1997). Such female counterstrategies may explain the absence of infanticide in species where it would be expected based on their life history (e.g. bonobos [*Pan paniscus*]: Hohmann et al., 2019; orang-utans [*Pongo spp.*]: chapter 4). Social counterstrategies to infanticide relate to getting the best protection for the infant from either male or female allies (Palombit, 2000; van Schaik and Kappeler, 1997). Besides establishing long lasting social bonds (review: Palombit, 2000; chacma baboons: Baniel et al., 2016; chimpanzees: Murray et al., 2016; olive baboons: Städele et al., 2019; bonobos: Tokuyama and Furuichi, 2016), it may also include secondary dispersal decision by females and group choice that reduces their infant's vulnerability to male selected infanticide (*Gorilla spp.*: Robbins and Robbins, 2018; Thomas langurs (*Presbytis thomasi*): Steenbeek, 2000). Sexual counterstrategies include manipulating i) males' paternity chances and ii) the information available to males, and thus their paternity assessments (assuming that males cannot recognize whether newborns are theirs—an assumption usually supported: van Schaik 2000). Females vulnerable to infanticide often exhibit long receptive periods, which allows for polyandrous mating. Several physiological adaptations have been linked to paternity confusion and promiscuous mating, including extended follicular phases, unpredictable ovulation and extended periods of fertility advertisement, such as exaggerated sexual swellings, which function as graded signals (Nunn, 1999; Zinner et al., 2004) and partly to attract reluctant subordinate males. Given that infanticide (or feticide, see: Zipple et al., 2019) often occurs when male dominance relationships change, females may limit their fitness losses by terminating maternal investment prematurely in such situations, also in the form of pregnancy resorption (reviews: van Noordwijk and van Schaik, 2000; Zipple et al., 2019).

The type of counterstrategies employed by female primates (and likely sires) depend on the source of the infanticide threat – either familiar or unfamiliar males – and hence, the social system (reviewed in Clarke et al., 2009). If the risk of infanticide stems from unfamiliar males, who may immigrate and become dominant (outside take-over), female counterstrategies are mostly social, while concentrating paternity probability into the dominant male to secure his protection of the infant (van Schaik et al., 2004). In species or populations with inside-group take-over risk, meaning that subordinate males may become dominant, females likely distribute paternity assessment among the males in such a way that males resume from killing or even protect their infant. Thus, females invest in both sexual and social counterstrategies (Clarke et al., 2009; van Schaik et al., 2004). Accordingly, sexual swellings which advertise fertility to males as graded signals are by a large found in multi-male-multi-female group-living species, where sexual counterstrategies to infanticide are needed to evade complete monopolization by the dominant male and distribute paternity across several males (Nunn, 1999; Zinner et al., 2004).

Because males profit from having accurate information on female reproductive state to assess siring probability, an informational arms race between the sexes may arise (van Schaik, 2016). Dominant males likely attempt to monopolize female sexuality to ensure siring her next offspring and so maximize their fitness, while females attempt to distribute paternity perception according to male dominance relationships to get the best protection for their infants, and so maximize theirs. Therefore, the optimal paternity likelihoods of the (dominant) male and a female are at odds, especially in multi-male-multi-female groups (van Schaik et al., 2004). While dominant males attempt to monopolize mating access to females, females may endeavour to distribute paternity assessment across several males. Males may attempt to control female sexuality by means of sexual coercion. In sum, the risk of infanticide shapes (primate) female sexuality (Nunn, 1999; van Schaik et al., 2000, 1999; Zinner et al., 2004) and by that the males' coercion potential (van Schaik et al., 2004). Therefore, the observed mating pattern is the outcome of this evolutionary arms race between the sexes to skew mating in their interest (Clarke et al., 2009; van Schaik et al., 2004). These theoretical approaches to link infanticide and sexual coercion are based on the assumption of delineated groups with one or more males with dominance hierarchies of known stability. The occurrence of sexually selected infanticide is mostly described in such social species and less frequent in solitary species (Lukas and Huchard, 2014). In species with no cohesive groups and a dispersed mating system, such as orang-utans, the observed patterns may reveal to be different.

Sexual coercion

Definition and different forms

Sexual coercion by males constrains female mating preference and thus, is the behavioural expression of sexual conflict (Pradhan and van Schaik, 2008). Smuts and Smuts (1993) defined it as the „*…use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female"*. Sexual coercion has been reported in many different animal taxa, ranging from insects (e.g. dragonflies (*Odonata*): Khelifa, 2017; tiger beetles (*Cicindelidae*): Parker, 1979) to waterfowls (Mineau et al., 1983) to mammals (Clutton-Brock and Parker, 1995; Muller and Wrangham, 2009), and takes different forms depending on the socio-ecology of the species (Muller and Wrangham, 2009; Smuts and Smuts, 1993; van Schaik et al., 2004). Several forms of male aggression qualify as sexual coercion: *Intimidation, harassment and forced copulations* (Clutton-Brock and Parker, 1995). Harassment, and in its extreme forced copulations, is aggression directed at a female which directly functions to increase a male's mating success with the female. Harassment is defined by repeated male mating attempts, which eventually lead to females giving in to the male's advances, whereas a forced copulation means that the "*male uses superior speed or strength*

to catch and physically restrain a female while he copulates with her by force" (Clutton-Brock and Parker, 1995). Intimidation may serve to punish females that refuse to mate and raise the male's chance that the female will mate with him in the future. Muller and Wrangham (2009) propose in addition to the direct forms of coercion (harassment, forced copulation and intimidation), also indirect coercion, including *coercive mate guarding, herding and sequestration,* which functions to decrease female promiscuity. However, one could argue these are all forms of harassment.

By the Smuts and Smuts' definition (1993) infanticide by males qualifies also as a form of sexual coercion, as the females incur high fitness costs when losing their infant (van Schaik et al., 2004). In this thesis, we take infanticide as a separate category of sexual conflict, which however is inherently linked to the expression of sexual coercion (see above). When referring to sexual coercion, we refer to male aggression directed at the female directly and not at her infant.

When females are vulnerable to sexual coercion and their counterstrategies

The occurrence of sexual coercion is the outcome of an evolutionary arms race between males attempting to control female sexuality and female counterstrategies (Pradhan and van Schaik, 2008). Comparative studies between various species and taxa on the occurrence and form of sexual coercion therefore help to understand in which context females are vulnerable to sexual coercion. Specifically, the risk of sexual coercion is higher if the males' physical strength is superior to that of the female, e.g. large sexual dimorphism, and female escape ability is low (Coercion Avoidance Hypothesis: Pradhan and van Schaik, 2009). Thus, sexual coercion is frequently reported in species or populations where females are isolated from conspecifics, and therefore lack protection by either male or female allies (Smuts and Smuts, 1993), and in diurnal, terrestrial species (Clarke et al., 2009; van Schaik et al., 2004). Accordingly, in species, where females are co-dominant to or dominant over males because either they form alliances with other females (vervet monkeys [*Chlorocebus aethiops*]: Andelman, 1987; Arseneau-Robar et al., 2016; e.g. bonobos [*Pan paniscus*]: Hohmann and Fruth, 2003) and/or size dimorphism is absent or even slightly reversed (e.g. lemurs: Kappeler, 2001), sexual coercion by males is mostly absent (see van Schaik, 2016). Female counterstrategies to sexual coercion overlap with the counterstrategies discussed in the infanticide part above (see above).

How to study sexual coercion? – Mating success and costs to female

Not all male aggression directed at females qualifies as sexual coercion. Male aggression against females may also occur in the feeding competition context, to establish dominance relationships, function as male policing, or be redirected aggression (reviewed in Muller et al., 2009). Moreover, male aggression, while meeting the criteria of the sexual coercion hypothesis, may not occur exclusively in the mating context. Thus, sexual coercion may not always be readily identifiable at first sight. To evaluate if male aggression functions as sexual coercion studies have focused on i) assessing if fertile females receive more male aggression, ii) relating rates of male aggression directed at a female and their mating rate or siring success and above all, iii) evaluating the fitness costs to the females as a result of male aggression.

Male aggression or the threat of force may occur decoupled from mating interactions, but still function as sexual coercion. Such decoupling of male aggression and mating interactions has most commonly been reported from polygynous systems, where males aggressively herd females during between group encounters to hinder them from transferring into another group (Western gorilla [*Gorilla gorilla gorilla*]: Breuer et al., 2016; hamadryas baboons [*Papio hamadryas*]: Swedell and Schreier, 2009). But also in multi-male-multi-female groups where males and females repeatedly interact, male aggression that functions as intimidation has been documented. In chacma baboons (*Papio ursinus*), males who direct most physical aggression towards females outside of the fertile period are more likely to consort females around conception, independent of the male's dominance rank (Baniel et al., 2017).

Similarly, Eastern chimpanzee males (*P. troglodytes schweinfurthii*) who direct most aggression towards cycling, non-periovulatory females get most mating solicitations by these females around ovulation, also independent of their dominance rank (Muller et al., 2011). Many studies evaluating if male aggression functions as sexual coercion have focused on mating success, and not on how this translates into actual siring success. Because of limited long-term data sets, studies on relating sexual coercion to male reproductive success in species with slow life history are rare. In Eastern chimpanzees, male aggression directed at periovulatory females leads to higher mating success, but only high-ranking chimpanzee males who directed more aggression towards cycling, but non-periovulatory females had higher siring success (Feldblum et al., 2014). Also in human hunter-gatherer societies, in-pair violence was reported to correlate with higher birth rates (Stieglitz et al., 2018).

Costs to females by male aggression range from injuries to constrained mate choice (Smuts and Smuts, 1993). Physical injuries are the most obvious cost to females resulting from sexual coercion by males, as reported in chimpanzees (Muller et al., 2007), chacma baboons (Baniel et al., 2017) and humans (Novak and Hatch, 2009). Yet, the costs from coercion may not always be apparent. First, male harassment may reduce female foraging efficiency and thereby lead to negative energy balances (chimpanzees: Emery-Thompson et al., 2014; dolphins [*Tursiops aduncus*]: Wallen et al., 2016). Second, female glucocorticoid levels were reported to be elevated in chimpanzees during the peri-ovulatory period when females experience most male aggression (Muller et al., 2007). Third, the risk of diseases transmitted during mating may pose another cost for the female (Nunn, 2003). Fourth, female mate choice is constrained by coercive males and may, hence, result in the reduced survival of her offspring (Clarke et al., 2009; van Schaik et al., 2004). Some studies also fail to find any costs for females by male aggression which was thought to function as sexual coercion (e.g. ritualized aggression). For example, gorilla females' stress levels were not increased around ovulation when they receive high levels of male aggressive displays (Habumuremyi et al., 2018). The authors concluded from this study that male displays at sexually active females rather function as courtship than coercion. However, sexual conflict in gorillas may rather be expected when it comes to female group affiliation (e.g. Robbins and Robbins, 2018). In any case, the absence of evidence is not evidence of the absence of costs to the female: Costs from male aggression may be diverse, subtle and hence, difficult to assess especially under field research conditions. Alternatively, rather than assessing females' costs directly incurred from male aggression, it appears crucial to evaluate the costs of female counterstrategies or resistance to male coercion. Such costs of female counterstrategies may provide information on how pronounced the underlying sexual conflict about paternity allocation is between males and females.

Potential for sexual conflict in orang-utans

In the primate order all forms of sexual coercion have been described (Muller and Wrangham, 2009), but only in orang-utans and humans forced copulations are frequently reported (MacKinnon, 1974; Thornhill and Thornhill, 1983). Orang-utan females have extremely long, variable inter-birth intervals of 6 to 9 years (van Noordwijk et al., 2018) and males are not territorial and roam widely, and in addition do not provide any direct paternal care to their offspring: all of this leads to an extremely high male-biased operational sex ratio. There is evidence for all three mechanisms of sexual selection – male-male competition, female choice and sexual conflict – shaping the orang-utan mating system (Fox, 1998; Spillmann, 2017). The large sexual dimorphism (Leigh and Shea, 1995), their semi-solitary lifestyle (Rijksen, 1978; van Schaik, 1999) and the absence of reliable fertility advertisement (Galdikas, 1981) make female orang-utans vulnerable to sexual coercion. Although forced copulations have been frequently observed in orang-utans, few studies have investigated the larger context of forced copulations in orang-utans, including its costs to females, the immediate context and consequences. With this thesis, we aimed to evaluate why and when forced copulations occur and to put them into the larger context of sexual conflict in orang-utans.

Orang-utans

Three orang-utan species are recognized by the IUCN since 2017 (*Pongo abelii* [Sumatran orang-utans]: Singleton et al., 2018; *Pongo pygmaeus* [Bornean orang-utans]: Ancrenaz et al., 2016; *Pongo tapanuliensis* [Tapanuli orang-utans]: Nowak et al., 2017), which are all listed as critically endangered (Figure 1). Their geographic distribution is limited to the islands of Sumatra (*P. abelii, P. tapanuliensis*) and Borneo (*P. pygmaeus,* divided into 3 subspecies) in South Eastern Asia. The third orang-utan species has only recently been described (Nater et al., 2017) and extremely little is known about the Tapanuli orang-utans' socio-ecology and how and to what extent it differs from the other two orang-utan species.

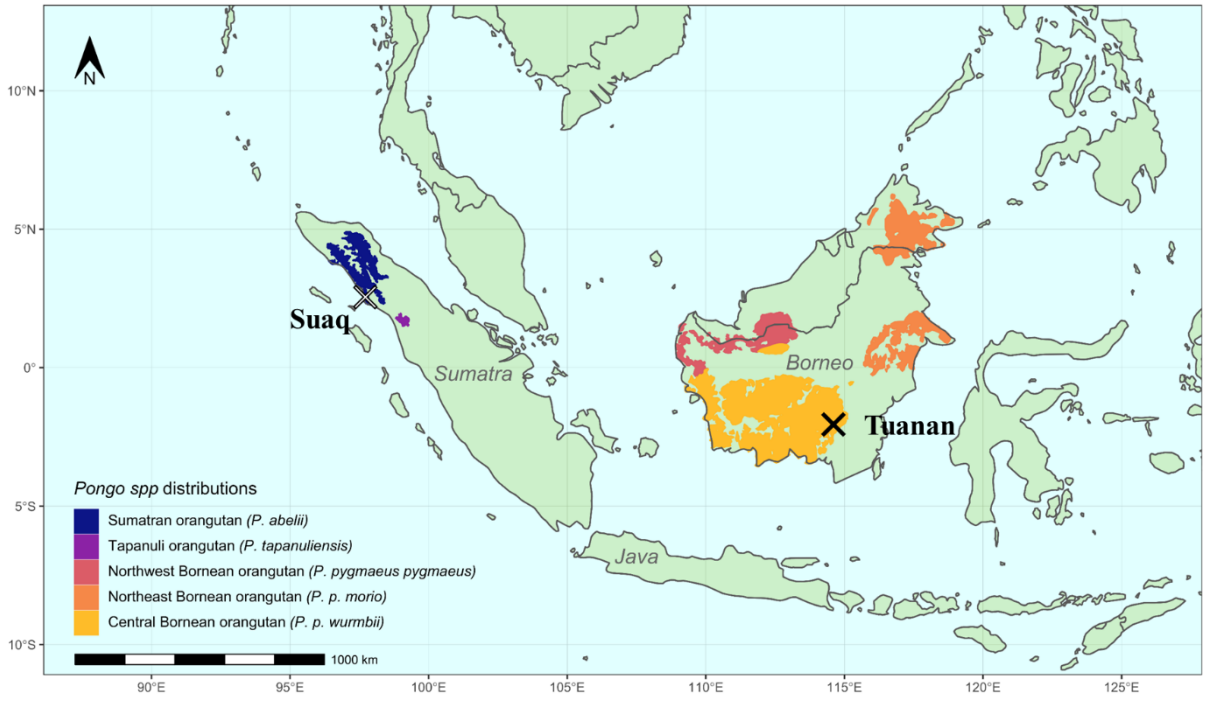


Figure 1 Geographic distribution of the three orang-utan species according to the distributions of the IUCN Red List of Threatened Species (Sumatran orang-utan [*P. abelii*] (Singleton et al., 2018), Tapanuli orang-utan [*P. tapanuliensis*] (Nowak et al., 2017), Bornean orang-utan [*P. pygmaeus*] (Ancrenaz et al., 2016)). The two long-term study sites where the data for this thesis were collected: Suaq, Aceh Selatan, Sumatra, and Tuanan, Central Kalimantan, Borneo, are indicated by black crosses (map created by A. Ashbury).

Orang-utans are at the solitary end of the fission-fusion spectrum (average daily party size ranges from 1.05 to 1.85 individuals) (Rijksen, 1978; van Schaik, 1999, Mitra Setia et al., 2009), and the only permanent association is between adult females and their dependent offspring (van Noordwijk et al., 2009). Female orang-utans are philopatric (Arora et al., 2012; van Noordwijk et al., 2012) and establish their home ranges close to their mother (Ashbury et al., in rev.; van Noordwijk et al., 2012). Males disperse after reaching independence from their mothers (Nietlisbach et al., 2012). Establishing male ranging patterns remains difficult, as they have very large home ranges, exceeding the size of both female home ranges and the study area (Singleton et al., 2009; Singleton and van Schaik, 2001).

Geographic variation in orang-utan socio-ecology and sexual coercion

Habitat productivity and variability in sociability

A large geographic variation has been described in orang-utan behaviour and physiology, which has been linked to habitat productivity (van Schaik et al., 2009a; Wich et al., 2011). In (West) Sumatran populations, where food availability is comparatively high, populations are more sociable and average

daily party sizes are larger than in Bornean populations (Mitra Setia et al., 2009; van Schaik, 1999). Accordingly, costs of association are assumed to be higher in populations with overall lower habitat productivity. In the genus *Pan*, this variation in habitat productivity and sociability can be linked to female sexuality and the occurrence of sexual coercion (Muller et al., 2011; Stumpf and Boesch, 2010): In the less sociable population, where the costs of association are higher, females experience male aggression more frequently. Here, we set out to compare two populations of orang-utans, one Sumatran (*P. abelii*) and one Bornean (*P. pygmaeus wurmbii*), both in the costs of association (chapter 3) and how this can be linked to the broader context of sexual conflict (infanticide: chapter 4), and the occurrence of sexual coercion (chapters 2, 5).

Absence of fertility advertisement and the cost of association

Orang-utan female reproductive physiology remains poorly understood (Knott et al., 2009). Females do not exhibit any morphological signal of fertility advertisement as other catarrhine primate females do with exaggerated sexual swellings (Nunn, 1999; Zinner et al., 2004). Yet, orang-utan females advertise pregnancy with small labial swellings (Galdikas, 1981). Although males are sometimes observed to investigate females' genitals, ovulation seems largely concealed from males, as they reportedly copulate independent of female ovulatory state (Knott et al., 2010; Nadler, 1981). Females may advertise fertility behaviourally by mating proceptively around the time of conception (Fox, 1998; Knott et al., 2010). Males who cannot rely on female choice likely use the size of a female's dependent infant (Cadilek, 2009; Fox, 1998) or the female's sexual behaviour as a proxy for her reproductive state. The consequences of the absence of fertility advertisements combined with the concealed ovulation are the topic of the fourth chapter of this thesis.

Male bimaturism

Orang-utan males exhibit irreversible bimaturism, unique in the primate order. The development of their secondary sexual characteristics (SSCs), including cheek pads (flanges), enlarged laryngeal sac, increased body size, long hair and the emission of long-calls, may be arrested up to 20 years (Utami Atmoko and van Hooff, 2004). The two male morphs, unflanged (pre-SSC) and flanged (SSC), have been associated with alternative reproductive strategies (Crofoot and Knott, n.d.; Galdikas, 1985a; Utami Atmoko and van Hooff, 2004). Flanged males are highly intolerant towards each other (Dunkel et al., 2013; MacKinnon, 1974; Mitani, 1985a; Spillmann, 2017), but tolerate unflanged males to some extent at a distance (Mitani, 1985a; Schürmann and van Hooff, 1986). Unflanged males are sometimes even reported to associate in bachelor groups and are more tolerant towards each other (Galdikas, 1985b; Reukauf, 2019; Sugardjito et al., 1987). While unflanged males have been associated with "go-and-search" or "sneak/rape" mating tactics, flanged males were labelled as engaging in "call-and-wait" or "combat/consort" (Galdikas, 1985b; Utami Atmoko and van Hooff, 2004). Accordingly, females are reported to approach the long calls of dominant flanged males in (West) Sumatran populations (Fox, 2002; Mitra Setia and van Schaik, 2007) and mate proceptively with them around the time of conception (Fox, 1998). In Bornean populations the long call function to mediate male-male competition has been established (Mitani, 1985b; Spillmann et al., 2017), whereas there is only limited evidence for a female attracting function (Mitani, 1985b; Spillmann et al., 2010). The lack of evidence may be due to small sample sizes, as a clear female preference for mating with flanged males has been reported (Borneo: Knott et al., 2010; O'Connell et al., 2019; Sumatra: Schürmann, 1981; Schürmann and van Hooff, 1986). Conversely, unflanged males are generally labelled as non-preferred by females both in Bornean and Sumatran populations, as they were reported to exhibit higher coercion rates based on population averages than flanged males (Knott, 2009; Knott and Kahlenberg, 2007; Utami Atmoko et al., 2009a).

The length of the developmental arrest of SSCs varies considerably among populations and species (*P. abelii, P. pygmaeus*) (Delgado and van Schaik, 2000; Dunkel et al., 2013). In Bornean populations, the unflanged to flanged male ratio is smaller than in Sumatran populations (Dunkel et al.,

2013), and there is more evidence for contest competition among flanged males (scars from physical fights: Dunkel et al., 2013; responses to long calls: Spillmann et al., 2017). The variation in developmental arrest can likely be linked to ecological factors, male dominance relationship stability and the monopolization potential in a population (Pradhan et al., 2012). The variation across study populations in coercion rates of the two male morphs, particularly flanged males, is perhaps related to the variability of the developmental arrest and the stability of male dominance relationships. Especially in Bornean populations, where the male dominance relationships fluctuate strongly, flanged males' proportion of forced copulations was on average reported to be higher than in Sumatran populations with a locally dominant flanged male (Knott, 2009; Knott and Kahlenberg, 2007; Utami Atmoko et al., 2009a). Most of these studies, however, are based on population and morph averages, and the resulting variation may therefore be an artefact of these averages over several individuals and low sample sizes. In the second chapter of this thesis, we set out to re-evaluate behavioural reproductive tactics of the two morphs based on individual males, including longitudinal data on six (nine) males who have transitioned from the unflanged to the flanged morph during the study period.

Table 1 Comparison between Bornean (*Pongo pygmaeus*) and Sumatran orang-utans (*Pongo abelii*) for various parameters relevant to understand male-female relationships and mating strategies.

	BORNEO		**SUMATRA**	
Fruit availability[1,2]	lower	**<**	higher	
Sociability[1,3]	lower	**<**	higher	
Cost of association	higher	**>**	lower	*Ch 3*
Length of consortships[4,5]	usually short	**<**	up to weeks	
Male dominance hierarchy[6,7]	unstable	**<**	stable	
Flanged : unflanged male ratio[7]	higher	**>**	lower	
Developmental arrest of SSC in males[7]	shorter	**<**	longer	
Mobility of flanged males (ground travel)[7,8]	higher	**>**	lower	
Confrontational assessment among flanged males[9,10]	common	**>**	rare	
Flanged males' tolerance towards unflanged males[11]	?	**<?**	Tolerated at distance	
Reproductive skew[12,13]	lower?	**<**	higher?	
Female mate preference[14,15]	flanged males that long call		Dominant flanged male	*Ch 4*

Footnotes:

1: van Schaik, 1999; 2: Wich et al., 2011; 3: Mitra Setia et al., 2009; 4: Schürmann and van Hooff, 1986; 5: Galdikas, 1985; 6: Delgado and van Schaik, 2000; 7: Dunkel et al., 2013; 8: Ashbury et al., 2015; 9: Mitani, 1985; 10: Spillmann et al., 2017; 11: Utami and van Hooff, 2004; 12: Borneo: Goossens et al., 2006, but see Tajima et al., 2018 and Banes et al., 2015; 13: Sumatra: Lenzi, 2014, but see Utami et al., 2002; 14: Borneo: Knott et al., 2010; Spillmann et al., 2010; 15: Sumatra Fox, 1998 and 2002, Mitra Setia and van Schaik, 2007.

Why do females resist?

The overarching question of this thesis was to understand why female orang-utans resist mating initiations by males. In other words, 1) when forced copulations occur, 2) why male and female interests are at odds in some instances and not others, and 3) why this may occur even within the same association dyad (Fox, 1998; Knott, 2009). Because males likely aim at fertilizing a female, when initiating copulations, their incentives, reproductive success, appear straight forward. The female's perspective is more obscure to orang-utan researchers. Several non-mutually exclusive hypotheses have been proposed to explain the negative female choice, as summarized in table 2. Previous studies have proposed that sexual coercion in orang-utans likely relates to the identity and morph of the male (Utami Atmoko et al., 2009a) and female reproductive state (Knott et al., 2010).

First, male quality may play a key role. Because unflanged males generally were reported to force a higher proportion of their copulations, the most common explanation for female resistance was the *Honest Resistance Hypothesis* (sensu Good Genes Hypothesis: Andersson, 1994). Females may resist mating initiations in general by males who they perceive of lower genetic quality (or less compatible with their own genes [Zeh and Zeh, 2001]). However, the *Honest Resistance Hypothesis* cannot explain why females may resist the same males at some instance and not the other, sometimes even within the same association unit (Knott, 2009). Thus, female resistance during sexual interaction may merely serve to assess male quality (*Assessment Hypothesis*). This would imply that females gain information on the males' condition, i.e. quality, by resisting and following their assessment either continue to resist or accept the males' mating initiation. Because orang-utans females' behaviour often appears ambiguous and was reported to change from resistance to passivity or even proceptivity and vice versa during the same interaction (Fox, 1998; Knott et al., 2010), the *Assessment Hypothesis* could not be conclusively excluded so far. If, however, females assess male quality with their resistance, forced copulations would by definition not qualify as sexual coercion (Smuts and Smuts, 1993) and not really be forced either. In chapter 2, we re-evaluate which males experience female resistance.

The *Infanticide Avoidance Hypothesis* can be seen as an extension of the male quality hypothesis. It predicts that female resistance varies with her reproductive state and the male identity or quality. Specifically, females are expected to adjust their resistance behaviour to minimize their infant's vulnerability to infanticide by males (van Schaik et al., 2000). Females are expected to concentrate paternity assessment onto males who pose the highest risk of future infanticide (van Schaik et al., 2004). When females are likely to conceive, they are therefore expected to resist to subordinate males (of "lower quality"), but to mate proceptively with dominant males. Such mating patterns have been reported from Bornean orang-utans (Knott, 2009; Knott et al., 2010). However, there is very limited evidence for the actual occurrence of infanticide in orang-utans both in the wild (Knott et al., 2019) and captivity (Mallinson, 1984), consistent with the existence of efficient female counterstrategies (Stumpf et al., 2008). Besides female mating behaviour, females have also been reported to avoid associations with males (Knott et al., 2018) and to maintain proximity to their infant when males are nearby (Scott et al., 2019). We elaborate on how female sexuality is consistent with counterstrategies to infanticide in chapter 4 and 5.

The *Price of Not Signalling Fertility* hypothesis relates the occurrence of forced copulations to the absence of reliable female fertility advertisements. Because male orang-utans do not have reliable signs of female reproductive state, they attempt to copulate even when a female is likely not fertile. The hypothesis follows the idea of the 'cost-of-sexual-attraction' hypothesis (Wrangham, 2002; details in chapter 3). Female orang-utans likely incur high costs from associations with both males and females as their low association frequencies indicate (Mitra Setia et al., 2009; van Schaik, 1999). If female orang-utans signalled fertility in regular cycles like other catarrhine primates with sexual swellings or other morphological signals (Nunn, 1999; Zinner et al., 2004), they would have repeatedly many male associates trying to mate with them and would thus incur high costs from these associations. In chapter 3, we evaluate the cost of association for females and in chapter 4, the consequences of the absence of fertility advertisement for the observed mating patterns.

The last two hypotheses presented suggest that the occurrence of forced copulations are a by-product of the reproductive physiology (4) or the habituation status of individuals (5). Both hypotheses are unlikely to explain the collision of male and female mating interests. First, previous studies report female resistance also around the timing of conception (Fox, 1998; Knott et al., 2010). Under the *by-product of reproductive physiology* hypothesis, however, female resistance would only be expected when a female is not fertile. Second, forced copulations were reported in captivity (Nadler, 1981) and involving very well habituated individuals in the wild (pers. obs.).

Table 2 Possible hypotheses why male and female interests may collide in orang-utans leading to forced copulations, with their predictions when coercion is expected depending on female reproductive status and the identity of the coercing male.

Hypothesis	**Scenario** (Figure 1)	**Female reproductive status**	**Identity of coercing males**	**Details in**
I. Male quality *(sensu Good Genes)*				
a. *Honest resistance*	Not you	NA	non-preferred male	*Ch 2*
b. *Assessment*	*Note: Would not qualify as sexual coercion*			
II. Infanticide avoidance	Not you Not now	peri-ovulatory period not receptive	non-preferred male any male	*Ch 4,5*
III. Price for not signalling fertility (artefact of cost of association)	Not now Not you	not receptive receptive	any male non-preferred male	*Ch 3,4*
IV. By-product of reproductive physiology (mismatch)	Not now	not receptive	any male	*Ch 4*
V. Artefact of habituation status	-	NA (unhabituated females)	unhabituated males	*unlikely*

The five hypotheses can be broken down into two main scenarios why male and female mating interests collide (Figure 2): the timing of mating (*"not now"*) and male identity (*"not you"*). On the one hand, forced copulations may occur during lactational infertility or outside of the peri-ovulatory period, which would be labelled as *"not now"*. On the other hand, if forced copulations occur around the timing of ovulation, it is likely a *"not you"* scenario. The two scenarios may interact, as proposed by the *Infanticide Avoidance Hypothesis* (reviewed in Knott, 2009).

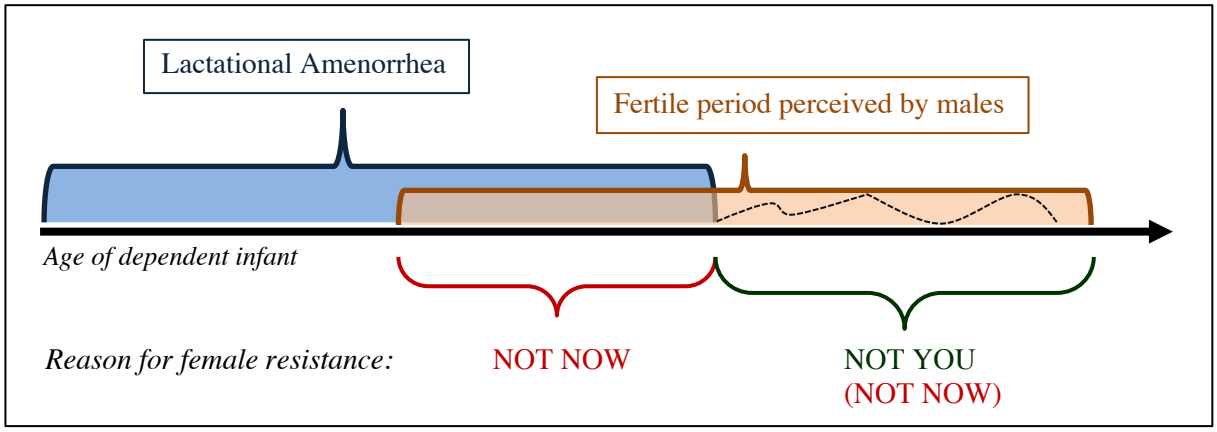


Figure 2: Illustration of possible scenarios (not now or not you) leading to mating conflict in orang-utans depending on the age of the females' dependent offspring (vertical axis), lactational infertility and the males' perception of female fertility. The dashed line after the lactational infertility indicates potential female cycles, although very little is known about when females resume to cycle in the wild. Thus, female preference may change also with these reproductive cycles (peri-ovulatory vs. not peri-ovulatory).

Contents of the thesis

This thesis consists of four empirical chapters (2-5) which are linked by the common goal of explaining female resistance to male mating initiations. The first three chapters set the basis by re-evaluating association and mating patterns using long-term behavioural and endocrine data based on separate individual identities. The fifth chapter analyses the effects of the immediate context of sexual coercion by males and female resistance.

Chapter 2: Alternative Reproductive Tactics of Unflanged and Flanged Males

In the second chapter, we re-visit the alternative reproductive strategies of the two male morphs combining longitudinal behavioural data on individual males who have transitioned from the unflanged to the flanged morph during the study period and cross-sectional data to compare how morph specific behaviour may vary between study sites and species. Previous studies reported a large variability of morph specific behavioural phenotypes across study sites and species (Knott, 2009; Utami Atmoko et al., 2009a) based on population wide morph averages. We evaluate association, copulation and coercion frequency of individual males and their morph state to decode if these reported differences are an artefact of averaging and small sample sizes or if in fact the behavioural difference between unflanged and flanged males in Borneo is less explicit than in (West) Sumatran populations.

Chapter 3: The Cost of Association with Males for Female Orang-utans

Sexual conflict in orang-utans may not only arise over mating itself, but also about associations and their maintenance. Female orang-utans do not advertise fertility with any apparent morphological signal (e.g. sexual swelling) like other catarrhine primates, but only show proceptive behaviour towards preferred males around ovulation (Knott et al., 2010), if at all. The absence of fertility advertisement may be explained by the high costs of association ('cost-of-sexual-attraction' hypothesis, Wrangham, 2002), but may make females vulnerable to sexual coercion. In the third chapter, we set out to analyse the costs of association to female orang-utans at two populations, one Sumatran (*P. abelii*) and one Bornean (*P. pygmaeus*), to evaluate if these may explain the absence of morphological fertility advertisements in the genus *Pongo*. We hypothesize that association maintenance may be another, more subtle context of sexual conflict in orang-utans. While females likely try to reduce the time in association with males, especially during the long period of lactational infertility, males may profit from associations with females i) to mate, ii) to monitor their reproductive state and sexual activities, iii) to attempt to monopolize female sexuality.

Chapter 4: Making Sense of Female Orang-utan Extended Sexuality

Female ovulation is largely concealed, besides her proceptive behaviour towards one preferred male (Fox, 1998; Knott et al., 2010) and therefore male orang-utans have no accurate cue when females are fertile. It seems paradoxical that female orang-utans do not advertise fertility reliably and thereby, reduce such costly associations with males (chapter 3), when females are highly unlikely to conceive. Unpredictable ovulation has been linked to the need for polyandrous mating serving paternity confusion to counteract the risk of infanticide. In the fourth chapter, we set out to evaluate individual female copulation and mating partner numbers for known conceptions to evaluate if female sexuality is congruent with such paternity confusion strategies. Besides the timing of mating interactions, we also evaluate the timing of female resistance relative to conception and how mating behaviour varied between female parity.

Chapter 5: The Immediate Context of Sexual Coercion

In the last empirical chapter of this thesis, we evaluated the immediate context of sexual coercion in orang-utans. Specifically, we test the relative importance of dyad composition and male-male competition on the occurrence of both male mating initiations and female resistance, while controlling for other factors which affect the occurrence of forced copulations, i.e. male morph (chapter 2), approximate female reproductive state (chapter 4) and fruit availability. Moreover, we assess the consequences of female resistance in terms of association maintenance and the arrival of other association members.

Study sites and methods

Because of their extraordinary slow life history and semi-solitary lifestyle, long-term data are necessary to reach conclusive results on the occurrence and context of sexual coercion in orang-utans. Limited sample size may be one reason for the enormous variability of reported mating patterns in orang-utans. We evaluated long-term behavioural and endocrine data of two study populations: Tuanan (*Pongo pygmaeus wurmbii*), Central Kalimantan, Borneo and Suaq (*Pongo abelii*), South Aceh, Sumatra (Figure 1). Behavioural data were collected by well-trained field assistants and students over 15 years (June 2003 – July 2018) at Tuanan and 11 years (June 2007 – March 2018) at Suaq, respectively, following a standardized protocol (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). Here, we provide background information on the behavioural data on sexual interactions. A detailed description of the data used for each separate section can be found in the corresponding chapters.

Behavioural data on sexual interactions

Sexual interactions were recorded whenever they occurred (all-occurrences sampling) and classified according to the female's behaviour (resisted, passive, proceptive) and whether intromission was achieved (copulation) or not (attempt) (for detailed definition see chapter 4, Table 9) (Fox, 1998). Whenever we refer to sexual interaction, it includes both copulations and attempts. Because female behaviour can be ambiguous within the same interaction (Knott et al., 2010), the categorization of sexual interactions can be tedious. Previous studies have categorized copulations as forced by the frequency of both female resistance and proceptive behaviour and male aggression (Fox, 1998; Knott et al., 2010). We took a more general approach and coded all interactions which involved any sign of female resistance behaviour as female-resisted (i.e. forced for the first 2 chapters). All other interactions were coded as non-resisted. If there was any sort of female proceptive act observed, the interaction was labelled as proceptive. Although reported in earlier studies, we did not observe any mating interaction where both female proceptive and resistance behaviour occurred, with the exception of two play interactions between a young nulliparous female and an unflanged male which led to a forced copulation. Interactions, however, often contained episodes when females were passive combined with either resistance or proceptive episodes. Whenever available, video recordings were taken into account to decide if female resistance was present or not during sexual interactions. Nevertheless, due to visibility constraints sometimes no video or detailed behavioural data were available. To sum up, because female and male behaviour during sexual interactions can be ambiguous, we cannot exclude that a minority of interactions may have been miss-classified. Nevertheless, we attempted to minimize such errors by excluding all interactions without sufficient observational data available. All interactions where the visibility was constrained by the canopy or because interactions occurred in tree nests were excluded from all the analyses.

Chapter 2: Reproductive Tactics of Unflanged and Flanged Male Orang-utans Revisited: A new longitudinal and cross-sectional analysis

Julia A. Kunz[1], Guilhem J. Duvot, Brigitte Spillmann[1], Erik P. Willems[1], Alison M. Ashbury[1], Maria A. van Noordwijk[1], Lynda P. Dunkel[1], Sri Suci Utami Atmoko[2], Carel P. van Schaik[1]

1) Department of Anthropology, University of Zurich, Switzerland
2) Faculty of Biology and Primates Research Center Universitas Nasional, Indonesia

Abstract

In many slowly developing mammal species, males usually reach sexual maturity well before they develop their secondary sexual characteristics (SSCs). Sexually mature male orang-utans exhibit extreme developmental arrest, which has been attributed to alternative reproductive tactics. We analysed long-term behavioural data from two study sites, Suaq (Sumatra, *Pongo abelii*) and Tuanan (Borneo, *Pongo pygmaeus wurmbii*), to assess male mating tactics in relation to study site, male morph (unflanged, flanged) and other socio-ecological parameters. Several individual males were observed to transition from the unflanged to the flanged morph, allowing us to assess changes in behavioural parameters. Both these longitudinal and our cross-sectional results based on individual males confirm previous cross-sectional accounts of the differences in mating tactics between the unflanged and the flanged male morphs. Relative to flanged males, unflanged males exhibit higher sociability, including with females, and higher rates of both copulation and coercion. Combined with previous studies of female reactions to long-calls and female choice for flanged males, we conclude that unflanged males follow a "*best-of-a-bad-job*" mating strategy. They are in a trade-off situation between needing to avoid male-male contest competition, but also needing to gain mating access to females.

Keywords: alternative reproductive tactics, developmental arrest, male bimaturism, sexual coercion

Introduction

Secondary Sexual Characteristics (SSCs) in male mammals may serve as weapons, badges of status for other males or ornaments to attract females (Darwin, 1871; Dixson et al., 2005; Grueter et al., 2015; Pradhan and van Schaik, 2009). Their development is generally delayed relative to sexual maturity (Irschick and Lailvaux, 2005; Wolff, 2008), as also found in catarrhine primates (Setchell and Lee, 2004). When the pre-SSC phase is unusually extended, this is thought to reflect an alternative reproductive strategy (Gross, 1996; Oliveira et al., 2008; Setchell and Dixson, 2001). Whereas male-male competition over access to fertile females is pronounced among the dominant SSC males, pre-SSC males are sometimes even tolerated by SSC males, allowing them to gain some reproductive success (primates: Setchell, 2008; mammals: Wolff, 2008). Therefore, because some delay in the development of the SSCs is inevitable, males use this period to obtain some reproductive success through alternative mating tactics (Gross, 1996).

A lengthy pre-SSC phase beyond the time needed to grow the SSCs is only expected if females have a clear preference for males with fully developed SSCs. This preference has been observed in many primate species (review: Andersson, 1994; Dixson et al., 2005; Pradhan and van Schaik, 2009; gorillas: Caillaud et al., 2008; orang-utans: Fox, 1998; vervet monkeys: Gerald et al., 2010; Verreaux's sifakas: Lewis and van Schaik, 2007; mandrills: Setchell, 2005). There are two main reasons for this female preference. First, they may reap indirect (genetic) benefits, because males who exhibit the SSCs have proven viable enough to survive (good genes hypothesis: Andersson, 1994) despite having to develop costly SSCs (e.g. Lüpold et al., 2019). Second, females may gain direct benefits through male protection. In species where the risk of infanticide and/or sexual coercion is high (Hrdy, 1979; van Schaik et al., 2004), females must rely on good protectors (Fox, 2002; Mesnick, 1997). Males with fully developed SSCs are generally dominant over pre-SSC males (Mitani, 1985a; Setchell and Dixson, 2001; Utami Atmoko et al., 2009b), and hence, while posing the highest threat for infanticide, are also the best protectors (Clarke et al., 2009; Mesnick, 1997; van Schaik et al., 2004).

Orang-utans exhibit an extraordinarily long pre-SSC phase. Unflanged males have fully developed testicles (Dahl et al., 1993) and have been shown to reproduce successfully in the wild (Goossens et al., 2006; Utami Atmoko et al., 2002). Eventually, they develop into flanged males with the SSCs, including cheek pads (i.e. flanges), increased body size (up to twice the size of female orang-utans), and an enlarged laryngeal sac, which enables them to emit long calls (Galdikas, 1985a; Kuze et al., 2005; Mitani, 1985b; Mitani et al., 1996). However, the unflanged stage may last for more than 20 years in the wild (Utami Atmoko and van Hooff, 2004), although in captive settings the development of SSCs may be accelerated (e.g Emery-Thompson et al., 2012; Maggioncalda et al., 1999). During the transition period from the unflanged to the flanged male morph (flanging), males exhibit a peak in testosterone levels (Maggioncalda et al., 1999; Marty et al., 2015). The development of SSCs is irreversible.

Orang-utans have extremely slow life histories (Wich et al., 2009); female orang-utans exhibit long and variable inter-birth intervals of 6 to 9 years (van Noordwijk et al., 2018) and have concealed ovulation (Knott et al., 2010; Nadler, 1981). Thus, the operational sex ratio is heavily male-biased, and siring opportunities are not only rare for males, but also scattered in space due to orang-utans' semi-solitary lifestyle (Rijksen, 1978; van Schaik, 1999).

Flanged males are mostly dominant over unflanged males and highly intolerant towards each other (Dunkel et al., 2013; Mitani, 1985b; Spillmann et al., 2017; Utami Atmoko et al., 2009b). Genetic evidence suggests that flanged males achieve most paternities (Banes et al., 2015; Goossens et al., 2006; Tajima et al., 2018), but this has not yet been confirmed under natural conditions. Studies have also shown that flanged males are preferred by females: (Receptive) females actively approach long calls of flanged males (Fox, 2002; Mitra Setia and van Schaik, 2007) and occasionally mate proceptively with

them (Fox, 1998; Knott et al., 2010; Schürmann, 1981; Schürmann and van Hooff, 1986). Thus, it has been suggested that flanged males follow a "call-and-wait" mating strategy (Utami Atmoko and van Hooff, 2004). However, long calls of flanged males may also attract potential competitors and have been shown to mediate male-male competition (Mitani, 1985b; Spillmann et al., 2017, 2010), which can lead to serious costs, such as injuries resulting from physical fights (Dunkel et al., 2013), but also allows females to mate with the strongest males. Evidently, given this female preference and greater competitive strength of flanged males, the pre-SSC phase would be a "best-of-a-bad-job" situation (Dawkins, 1980), and it would be advantageous to pass through it as rapidly as possible.

Unflanged males have lower reproductive success than flanged males (Utami Atmoko et al., 2009a). They are more tolerant towards each other, especially in Sumatran populations (Galdikas, 1985b; Sugardjito et al., 1987), and being faster in the trees are often tolerated by flanged males (Mitani, 1985a; Schürmann and van Hooff, 1986). Unflanged males do not emit long calls, and roam widely to search for and associate with females ("go-and-search" strategy) (Utami Atmoko and van Hooff, 2004) and are far more likely to engage in forced copulations (Fox, 1998; Galdikas, 1985b; MacKinnon, 1974; Utami Atmoko et al., 2009a; Utami Atmoko and van Hooff, 2004), a common form of sexual coercion (Clutton-Brock and Parker, 1995; Smuts and Smuts, 1993). Nevertheless, females may also mate cooperatively with unflanged males or resist flanged males (Knott, 2009; Utami Atmoko et al., 2009a). This ambiguity of female resistance has been linked to their reproductive status and ultimately may function as a female infanticide avoidance strategy (for details see Knott et al., 2010).

Given their reduced reproductive success and attractivity to females, the extended period that males spend as the unflanged morph (pre-SSC) appears paradoxical. Pradhan et al. (2012) presented a model that attributes the long developmental arrest in male orang-utans to i) a highly male-biased operational sex ratio and thus intense male-male contest competition over access to females, ii) high monopolization potential by dominant males, and iii) low male mortality, combined with iv) a not-quite-zero rate of reproductive success for pre-SSC males. Paternity data suggest that pre-SSC males sire some first offspring of adolescent females (Goossens et al., 2006; Utami Atmoko et al., 2002). Thus, males would do better remaining unflanged if they cannot become dominant. A shorter delay would be selected for if the monopolization potential of the dominant (flanged) male in a population falls below a threshold value, which would allow other flanged males to gain enough paternities to make the switch worthwhile. Accordingly, the data suggest that in (West) Sumatran populations, which have a higher monopolization potential, the developmental arrest is more pronounced than in Bornean populations (Delgado and van Schaik, 2000; Dunkel et al., 2013).

The overall picture of the reproductive tactics of these two morphs and the patterns of developmental arrest among male orang-utans is uncertain. Considerable variation is reported between sites and islands in the patterns reviewed above (Knott, 2009; Utami Atmoko et al., 2009a), which may reflect true variation or problems with previous work. Many previous studies suffered from small sample sizes, and were therefore limited in the extent to which they could control for confounding variables, and avoid such problems as pseudo-replication arising from having to lump individuals or even classes of individuals. Moreover, previous work consists entirely of cross-sectional comparisons; so far, we lack longitudinal behavioural evidence for the change(s) in an individual's mating tactics with the development of SSCs.

We aim to understand how behavioural reproductive tactics of adult male orang-utans vary based on their morph and their socio-ecological context. To this end, we combine a within-individual longitudinal analysis with a cross-sectional comparison with the same population and between two populations. Based on earlier studies, we predict that males will have higher association rates and longer associations, especially with nulliparous females, while they are unflanged than after their development of SSCs. During associations, unflanged males are expected to be in closer proximity to females, given

that they cannot rely on female proceptivity and may use association opportunities both to mate and to monitor female fertility status and sexual activities. Accordingly, we predict higher copulation rates and more frequent sexual coercion by unflanged than by flanged males.

Additionally, we conducted an extensive cross-sectional comparison of individual unflanged and flanged male behaviour in two populations, one on Sumatra (*Pongo abelii*) and one on Borneo (*Pongo pygmaeus wurmbii*), to understand the variation not only between male morphs, but also across sites with different socio-ecological contexts (van Schaik, 1999; Wich et al., 2011). As suggested by previous studies (Mitra Setia et al., 2009; van Schaik, 1999), we expect higher association and copulation frequencies among both unflanged and flanged males in the Sumatran population compared to the Bornean population. Unflanged males in the Sumatran population are expected to force a higher proportion of their copulations than unflanged males of the Bornean population (Knott, 2009; Utami Atmoko et al., 2009b), because of the more pronounced female preference for the dominant flanged male on Sumatra. Forced copulation rates by flanged males are predicted to be higher in the Bornean than the Sumatran population (Knott, 2009; Utami Atmoko et al., 2009b) due to the less pronounced developmental arrest, the unstable male dominance relationships and thus, increased male competition (Dunkel et al., 2013; Spillmann et al., 2017).

Methods

Study sites and study subjects

We analysed long-term behavioural data from two study sites: Tuanan, Mawas Reserve, Central Kalimantan, Indonesia (02°15'S; 114°44'E) and Suaq, Gunung Leuser National Park, South Aceh, Indonesia (03°02'N; 97°25'E). From Tuanan, we included a total of 25 374 focal follow hours of adult males and 41 713 focal follow hours of adult and adolescent females, collected between June 2003 and July 2018, in the analysis. From Suaq, we included a total of 3 815 focal follow hours of adult males and 8 504 focal follow hours of adult and adolescent females, collected between June 2007 and March 2018, in the analysis. At both sites, behavioural data were collected by well-trained observers using the same standardized protocol.

Because of the continuous long-term data collection effort, subjects were individually recognized and we could collect longitudinal data of six males in both the unflanged and the flanged morph status. We determined individual identity by visual inspection of photographs as well as genetic data (Arora et al., 2012; Krützen, pers.comm.; for details also see: Dunkel et al., 2013). Because orang-utan males roam widely (Singleton et al., 2009; Singleton and van Schaik, 2001) and are often absent from the study area for extended periods (Utami Atmoko et al., 2009b), their identification can be problematic. Therefore, we only included males that were identified with certainty by several independent observers in the analyses. We placed the males observed during the period when they developed their SCCs ("flanging males") in the unflanged male morph category in the analyses. Because males were rarely observed during the actual development of the SSCs (total of 48 observation hours) (Marty et al., 2015), there was not enough data available to include developing males as a separate category.

We subdivided females into two classes according to their parity status: *nulliparous females* comprised all adolescent females that were known to be sexually active but had not yet given birth to their first offspring. *Parous females* included all adult females with a known dependent offspring between 0 and 8 years of age, as well as females without any dependent offspring, because their youngest offspring was either older than 8 years of age and weaned or, in rare cases, had died (van Noordwijk et al., 2018).

Behavioural data

Focal animal behavioural data were collected according to an established protocol (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). Association partners (all individuals within 50 meters of the focal animal) were noted at 2-minute intervals. However, evidence suggests that orang-utans can perceive each other at larger distances than 50 m (van Noordwijk et al., 2012, 2009) and thus, short-term interruptions of the <50 m distance are likely not indicative of an association ending and re-starting, from the orang-utans' point of view. We therefore define a male-female association unit as a male-female dyad which did not separate for more than one known full-day focal follow outside of the <50 m periphery. An association unit, therefore, may last over several consecutive days and may comprise breaks, when the association partners were at more than 50 m distance.

We recorded all occurrences of sexual interactions and the identity of the individuals involved (Altmann, 1974). Despite over 79 000 focal hours at the two sites combined, male-female associations (N=2107 [Suaq: 618; Tuanan: 1489]) and, in particular, copulations (N=482 [Suaq: 164; Tuanan: 318]) were rare. We therefore combined data to analyse copulation and coercion frequencies of individual males from both focal adult male follows (>29 000 hours) and focal female follows (>50 000 hours), when the males were association partners. The frequencies were corrected for sampling effort by calculating the total time that a specific individual was observed (*observation time* = sum of the individual's focal follow hours and the time in association with a female when not the focal animal). To avoid introducing a bias towards males who are frequently observed in association, each male's total association time with females was included as an additional control variable in the analyses.

We only counted sexual interactions with achieved intromission as copulations. All failed copulation attempts, i.e. when no intromission was achieved, were excluded from the analyses (9.7% of all sexual interactions were attempts). Copulations were labelled as *forced* if there was any sign of female resistance throughout the sexual interaction. Female resistance behaviour could manifest in (repeated) attempt(s) to move away from the male, obstructing the male's attempt to position the female for intromission, slapping and biting the male to evade intromission, and was often, but not always, accompanied by the female emitting squeal or scream vocalizations (Fox, 1998; Knott et al., 2010). All copulations without apparent female resistance were labelled as *unforced* copulations. *Proceptive* copulations, wherein the female initiated the copulation, were a subcategory of *unforced* copulations and were rare (Table 3).

Ecological data

As an ecological proxy for food availability, the monthly Fruit Availability Index (FAI) was included in the analyses (cf. Harrison et al., 2010; Vogel et al., 2017). FAI is the percentage of trees bearing fruits, of all the surveyed trees (Suaq: ~1000 trees; Tuanan ~1500 trees). Monthly FAIs were available for both study sites over the entire study period. Because the FAIs are generally higher at Suaq than Tuanan, we standardized the values within site using z-transformations. In the results, the FAI is called "zFAI" to indicate this transformation.

Statistical analyses

We conducted all statistical analyses in R (R Core Team, 2018), using the packages 'lme4' and 'lmerTest' (Bates et al., 2015; Kuznetsova et al., 2017) to formulate (generalized) linear mixed models ([G]LMMs). Residuals of *Gaussian* models were checked for normality and homoscedasticity by visual inspection of residual plots. Additionally, all models were examined for multi-collinearity (Variance Inflation Factor < 2) and influential cases (Fox and Weisberg 2018). Furthermore, models with a Poisson distribution were tested for over-dispersion. Here, we report the full models tested including all control and fixed effects, the (pseudo-) R^2 as obtained from the 'MuMIn' package (Barton, 2018), and the comparison to the null model, containing all random intercepts and control factors.

Association patterns

Cross-sectional data

Because an association is a prerequisite for a copulation to occur, we first analysed the association patterns of males. First, we set up a Poisson GLMM with the number of different females in association on a given male full-day focal follow as a response variable (N=807 days), independent of the actual association duration. We included site (Suaq vs. Tuanan), male morph (unflanged vs. flanged) and local zFAI as fixed effects and added the male identity and the male specific follow period, which comprised individual male follows in 3-months blocks, as a random intercept to account for pseudo-replication. Second, 1) the association duration (hours) and 2) the time spent in close proximity (<10m) to female association partners were assessed in respect to site, male morph, female class and zFAI. Because association units were taken as response variable, we account for having the same individuals and dyads several times in the analyses by adding both male and female identity as crossed random intercepts in the model. We included only dyadic associations with known start and end in the analyses, with the exception of long association units. Focal animals are usually not followed for more than 10 days in a row to avoid over-habituation effects (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). To refrain from biasing the analyses against long associations caused by giving up following long associations, the association dyad was still included in the analyses if the dyad was still in association when the focal follow ended and/or was found together. Association duration was defined as the total active hours a dyad was followed and known to be within 50 m (either the male or the female or both were followed) and did not include neither night hours if a dyadic male-female association lasted overnight nor breaks when the association dyad was at a larger distance than 50 m during the focal follow. The association hours were normalized for the analysis by natural logarithm-transformations.

Longitudinal data

The analyses based on the full-day focal follows as described above for the cross-sectional data was repeated with the subset of the data containing only the males for which data of both morph state were available. To compare the proportion of the total observation time spent in association with females within individual males in their unflanged and flanged status, we ran a linear model with the morph as a fixed effect. Further, we conducted a linear mixed effects model with the male identity as a random intercept to assess the proportion of association time males spent in close proximity (<10m) of females.

Copulation frequency

Cross-sectional data

We formulated a Poisson generalized linear mixed model (GLMM) to assess the total number of observed copulations per male (corrected for observation effort). We used the all-occurrence data set for copulations and the total observation time per male identity and morph. We included only individually recognized males for which at least 100 observation hours were available for a particular morph (unflanged or flanged) (N=66). Not all males were observed to copulate during these 100 observation hours (suppl. mat. Sfigure 2). We included the total observation time of each male as an offset term in the model to correct for differences due to sampling effort using the log-link function. We set study site, male morph and the z-transformed association time with adult females as fixed factors. We tested possible interactions between the fixed factors. Male identity was added as a random intercept, because some males were represented twice in the model, as they developed their SSCs during the study period.

Longitudinal data

The differences in copulation frequency between the unflanged and flanged status within individual males were assessed using a Poisson generalized linear model (GLM). We accounted for the

problem of over-dispersion by using the "quasi-Poisson" family. The total association time with females, the male morph and the individual identity were set as fixed effects. Because of the small data set (N=6 individual males), we could not include individual identity as a random intercept. Unfortunately, we could not assess any site difference in the longitudinal analyses due to a lack of data for the Suaq population (only one individual who developed flanges during the study period had enough data for both morph states). We therefore conducted the analyses both with and without the Suaq individual (for the results excluding the Suaq individual see suppl. mat.).

Forced copulation frequency

Cross-sectional data

The proportion of forced copulations (out of all observed copulations) by individual males was analysed in a "quasi-binomial" generalized linear model (GLM). The "quasi" family was chosen to account for the over-dispersion of the data. Only males who could be identified with certainty and who were observed to copulate were included in the analyses (N=65 individual males). To avoid pseudo-replication by having the males who had developed SSCs during the study period twice in the analysis, we conducted the analyses twice – once with them in the unflanged and once in the flanged morph. Only one male who had developed SSCs was observed to copulated in both morph states and the patterns were not different in the two analyses. In the results, we report the analysis with him in the flanged morph (for the results including him in the unflanged morph see suppl. mat. Stable 8). We included observation time as a weighting variable, so that data points consisting of more observation hours were weighted stronger in the analysis to account for the high variability in observation hours between individuals as a result of the males' varying presence in the study area. Copulations with both nulliparous and parous females were included. Additionally, the study site, the male morph and the total time in association with females (z-transformed) were added as fixed factors in the model. The total number of copulations could not be added to the model as a control factor due to collinearity with the time in association with females (VIF > 6). Because only one male who developed his SSCs during the study period was observed to copulate at all as flanged male, we could not conduct this analysis with the longitudinal data set.

Results

Association patterns – cross-sectional data

Unflanged males were in association with females 45.5 ±2.7 % (mean ± SE) at Suaq and 39.0 ±3.7 % at Tuanan of their total observation time. Conversely, flanged males were only observed in association with females 18.3 (±SE 4.2) % at Suaq and 10.3 (±SE 1.8) % at Tuanan of their observation time (Figure 3). On the basis of full-day focal follows and independent of the association duration (see below), unflanged males had a higher average number of different females in association per day (Suaq: 0.83 ±SE 0.15 females; Tuanan: 0.79 ±SE 0.06) than flanged males (Suaq: 0.45 ±SE 0.10; Tuanan: 0.24 ±SE 0.02) ($\beta_{unflanged\ vs.\ flanged}$= -1.09±0.14, t= -7.61, P<0.001). The number of females in association increased with local fruit availability (β_{zFAI}= 0.14±0.07, t= 2.13, P=0.03). It was not significantly different between the two sites ($\beta_{Suaq\ vs.\ Tuanan}$= -0.32±0.21, t= -1.53, P=0.13), but this lack of site difference may reflect the small sample size for Suaq (N=23 unflanged and 54 flanged male full-day focal follows). The full model for the number of female associates was significantly better than the null model ($\chi^2_{3,6}$ = 60.53, P<0.0001, pseudo-R^2 = 0.19; N=807 full-day focal follows of 92 male identities and 307 different follow periods; suppl. mat. Stable 1).

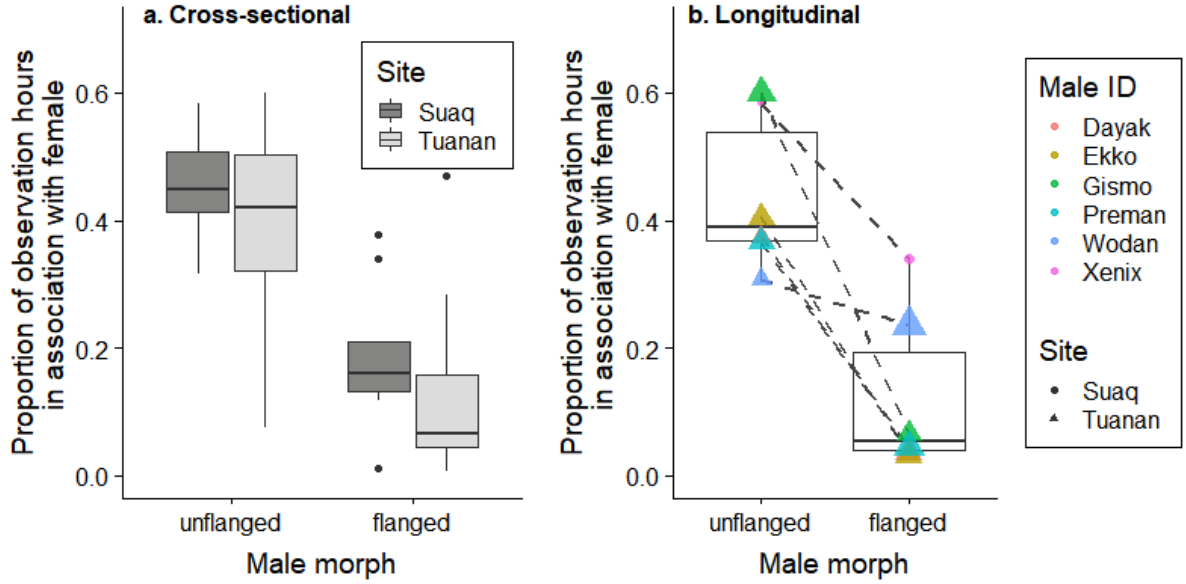


Figure 3 Difference of association rates with females (proportion of time per observation hour) between unflanged and flanged males: a) Cross-sectional data from the two study populations Suaq (*P. abelii*) and Tuanan (*P. pygmaeus*); the boxplots are based on the median association rate over all the individual males per study site and morph. b) Longitudinal data showing the males that developed SSCs during the study period: The dashed lines and coloured dots indicate the within-individual change in association rate from the unflanged to the flanged morph (Note: only Xenix is from the Suaq population). The size of the data points is proportional to the number of observation hours for individual males (and morphs). The boxplots are based on the median association rate per male morph and the populations are lumped.

The duration of male-female associations was generally longer with unflanged (Suaq: 5.04 ±SE 1.13 h; Tuanan: 5.65 ±SE 0.43 h) than flanged males (Suaq: 1.41 ±SE 0.41 h; Tuanan: 0.92 ±SE 0.12 h). There was a significant interaction between male morph and female parity: Unflanged males remained relatively longer in association with nulliparous than parous females, while flanged males' association duration did not vary with female parity ($\beta_{Male\ morph*Parity}$=0.39±0.17, t=2.24, P=0.03). Overall, the full model for male-female association duration was significantly better than the null model ($\chi^2_{5,12}$ = 30.47, P<0.0001, pseudo-R^2=0.22; suppl. mat. Stable 2). Further, unflanged males also spent more time in proximity (<10m) of females than flanged males ($ß_{unflanged\ vs.\ flanged}$=-0.18±0.02, t=-10.20, P<0.001). The full model for the proportion of association time in close proximity was significantly better than the null

model ($\chi^2_{3,7}$=123.59, P<0.0001, N=1324 dyadic associations including 203 different males; suppl. mat. Stable 2; Figure 4).

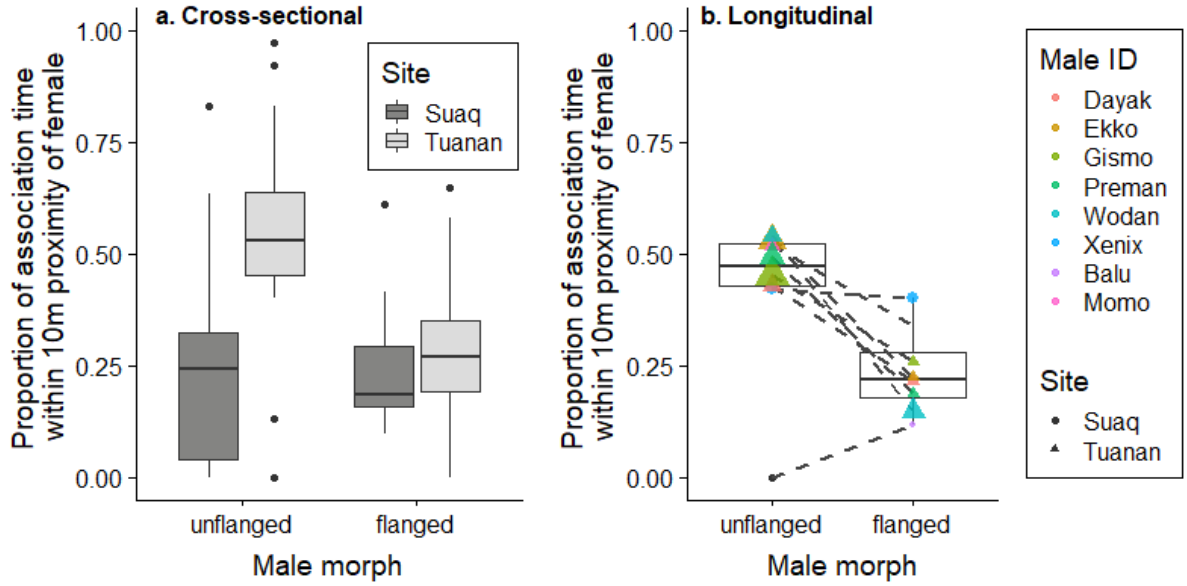


Figure 4 Proportion of association time within 10m proximity to those female association partner by unflanged and the flanged males: a) Cross-sectional data from the two study populations Suaq (*P. abelii*) and Tuanan (*P. pygmaeus*); the boxplots are based on the median proportion of association time spent in proximity over all the individuals (average per male-morph point) per study site and morph. b) Longitudinal data on the proportion of association time spent in proximity to females by individual and morph average: The coloured data points indicate the males which were observed in association as both unflanged and flanged males (circles: Suaq, triangles: Tuanan; the size of the data points is proportional to the association hours of a male [and morph]). The dashed lines connect the same individual from the unflanged to the flanged morph. The boxplot represents the median time spent within 10m of a female over all the males and populations shown in figure b. (Note: The number of males over the transition from unflanged to flanged is increased [N=8] compared to Fig. 1 and 3, because all the data available on male-female associations was included, regardless of the follow hours available).

Association patterns – longitudinal data

Our analysis of the subset of the data containing only individuals for which data on the unflanged and the flanged morph were available revealed the same association patterns as the cross-sectional analysis. In the unflanged morph, males had on average more females in association on full-day focal follows (0.84±SE 0.09 females per day [85 full-day focal follows of 6 males]) than when they were flanged (0.21±SE 0.03 females per day [165 full-day focal follows of 6 males]) ($\beta_{\text{unflanged vs. flanged}}$= -1.17±SE 0.23, z=-5.09, P<0.001). Also, in the longitudinal subset, the number of daily female associates tended to increase with local FAI (β_{zFAI}=0.19 ±SE 0.11, z=1.76, P=0.08), but there was no difference between sites ($\beta_{\text{Suaq vs. Tuanan}}$=-0.20 ±SE 0.64, z=-0.31, P=0.76). Whereas site differences were unlikely to show up in the longitudinal analyses, because only one male from Suaq (Xenix) was included. The full model was significantly better than the null model ($\chi^2_{3,6}$=33.75, P<0.001; N=250 full-day focal follows of 6 male IDs and 82 follow periods; suppl. mat. Stable 4) and including interactions between neither site and morph nor morph and local FAI did not improve the model fit.

Furthermore, individual males spent significantly more time in association with females when unflanged (43.9±SE 5.0 % of observation time in association with females) than when they were flanged (12.6±SE 5.3 % of observation time in association with females) ($\beta_{\text{unflanged vs. flanged}}$= -0.31±SE 0.07, t= -4.30, P=0.003; $F_{1,10}$=18.48, P=0.002, N=12 [6 IDs]) (Figure 3). Between-individual variation did not improve the model fit for the proportion of time spent in association with females (F=2.26, P=0.2; suppl. mat. Stable 4). During associations, males spent significantly more time within 10m proximity of females when unflanged than when they were flanged ($\beta_{\text{unflanged vs. flanged}}$=-0.16±SE 0.06, t=-2.60, P=0.03)

(Figure 4). To sum up, the decrease in association frequency and duration with females from the unflanged to the flanged male morph was confirmed with the longitudinal data set.

Copulation frequency – cross-sectional data

Unflanged males copulated more frequently both at Suaq (Suaq: 0.035 [mean] ± SE 0.009 cop/h [copulations per observation hour]) and Tuanan (Tuanan: 0.035±SE 0.005 cop/h) than flanged males (Suaq: 0.005±SE 0.004 cop/h; Tuanan: 0.003±SE 0.001 cop/h) ($\beta_{\text{unflanged vs. flanged}}$=-2.78±SE 0.30, z= -9.27, P<0.001) (Figure 5). Overall the total association time with females increased with the number of copulations observed for an individual male ($\beta_{\text{zAssociation with females}}$=0.23±SE 0.11, z=2.01, P=0.05). The individual male copulation frequency did not differ between the two study sites ($\beta_{\text{Suaq vs. Tuanan}}$= -0.09±SE 0.33, z=-0.28, ns.) and the interaction between morph and site did not improve the model fit ($\chi^2_{5,6}$=0.86, P=0.35). The full model for the copulation number was significantly better than the null model ($\chi^2_{2,5}$=121.4, P<0.0001, pseudo-R^2=0.95; N=66 morph-identity points of 58 different males; suppl. mat. Stable 6). The dominant flanged male, Islo, of the Suaq population was an outlier with his 30 total copulations. When excluding Islo from the analyses (suppl. mat. Stable 7), the only significant difference in copulation frequency was between unflanged and flanged males ($\beta_{\text{unflanged vs. flanged}}$ =-2.93±SE 0.29, z=-10.191, P<0.0001, N=65 of 57 different males), but neither dependent on the site ($\beta_{\text{Suaq vs. Tuanan}}$= -0.20±SE 0.32, z=0.64, ns.) nor the time spent in association with adult females ($\beta_{\text{zAssociation with females}}$=0.12±SE 0.10, z=1.18, ns.). Further, a flanged male from Tuanan, Wodan, was also an outlier. He was observed in a long consortship with a parous female (more than 10 consecutive days) during which they did not copulate. Thus, his overall association time with adult females was relatively high, but no copulations were observed. However, excluding him from the analyses did not change the pattern.

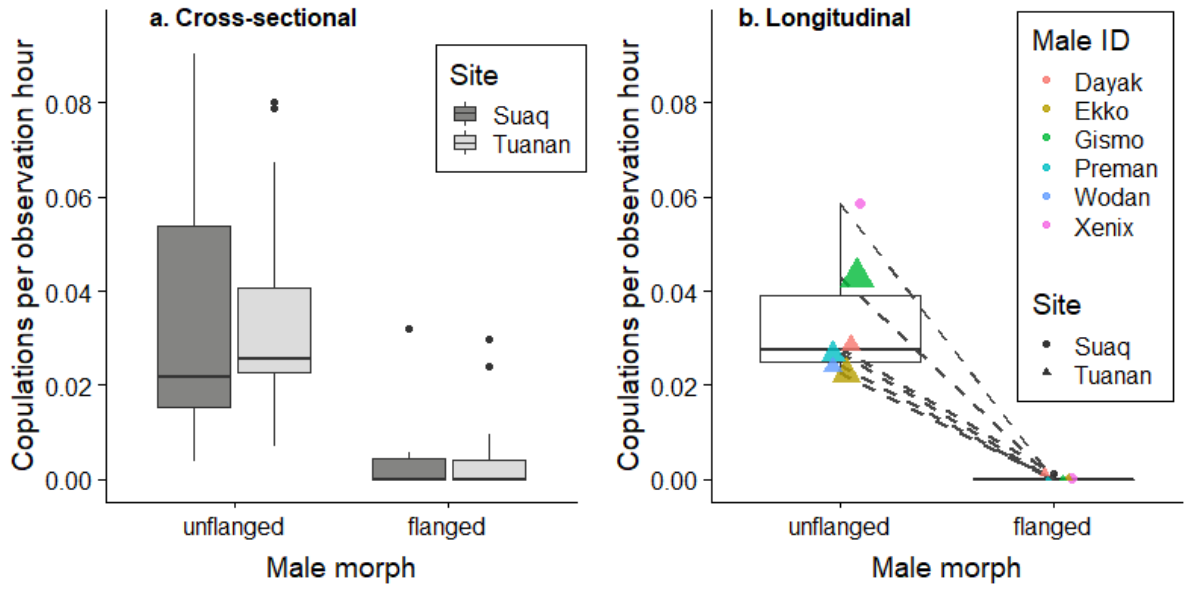


Figure 5 Difference of copulation frequency (copulations per observation hour) between unflanged and flanged males: a) cross-sectional data based on individual male copulation frequency. The boxplots are based on the median copulation frequency per male morph and study population (*colour*). b) longitudinal data illustrating the within-individual change in copulation frequency from the unflanged to the flanged male morph (dashed lines): Each male is illustrated in a different colour and the point characters indicate their study site (circle: Suaq; triangle: Tuanan) (*Note:* only Xenix is from the Suaq population. Dayak's copulation rate as flanged male was 0.001 cop/h). The size of the data points is relative to the time individual males (and morphs) have spent with adult females. The boxplots are based on the median copulation frequency over all the six males (from both study sites) by their morph.

Copulation frequency – longitudinal data

The copulation frequency of unflanged males decreased drastically after they became flanged ($\beta_{\text{unflanged vs. flanged}}$= -4.92±SE 1.31, t= -3.76, P<0.0001) (Figure 5), even when controlling for their reduced total association hours with adult females (i.e. copulation opportunities) ($\beta_{\text{zAssociation with females}}$= 0.08±SE 0.07, t=1.19, P=0.26). Accordingly, the model fit improved when including male morph (χ^2_1=117.34, P<0.0001; suppl. mat. Stable 4). Except for one male (Dayak, copulation rate=0.001 cop/h, Fig. 3), none of the males for which data for both male morph periods were available was observed to copulate in the flanged morph. One male (Gismo) appeared to be an outlier, exhibiting very high copulation rates as an unflanged male. Excluding him from the analyses, however, did not change the pattern. Thus, the cross-sectional decline in copulation frequency from the unflanged to the flanged male morph was validated by the within-individual decrease of copulation frequency after the development of SSCs.

Forced copulation frequency – cross-sectional data

Individual males (N=65 males and 393 copulations) forced on average 41.9±SE 4.8% (Suaq [N=27]: 64.8±SE 7.5%; Tuanan [N=38]: 25.7±SE 4.8%) of all their copulations (Tab. 1). Unflanged males forced a higher proportion of their copulations (Suaq: 0.75±SE 0.07 [N=22]; Tuanan: 0.30±SE 0.05 [N=24]) than flanged males (Suaq: 0.21±SE 0.20 [N=5]; Tuanan: 0.18±SE 0.10 [N=14]) ($\beta_{\text{unflanged vs .flanged}}$= -1.75±SE 0.36, t= -4.81, P<0.001) (Figure 6). Moreover, males at Tuanan forced fewer copulations than at Suaq ($\beta_{\text{Suaq vs. Tuanan}}$= -0.80±SE 0.35, t= -2.30, P=0.03). The time in association with females did not predict the proportion of forced copulations ($\beta_{\text{zAssociation with females}}$= -0.03±SE 0.06, t= -0.45, P=0.65). The full model was significantly better than the null model (χ^2_3=13243, P<0.001; suppl. mat. Stable 9). Furthermore, the interaction between male morph and site significantly improved the model fit (χ^2_1=6955, P<0.001; suppl. mat. Stable 9), indicating that unflanged males forced a higher proportion of their copulations compared to flanged males at Suaq than at Tuanan ($\beta_{\text{Site*Morph}}$= 3.36±SE 0.80, t= 4.26, P<0.001). Importantly, individual unflanged males were observed to have both forced and unforced copulations (Figure 6). Most of the unflanged males who were observed to force all of their copulations (11 of 45 unflanged males) were observed to copulate only once or twice in total (7 of 11 unflanged males). Unflanged males who were observed to copulate at least 3 times in total (N=36 individuals), forced on average 44.8±SE 5.2% (Suaq: 71.1±SE 7.3%; Tuanan: 28.2±SE 4.3%) of their copulations and only four of these unflanged males forced all of their copulations. In conclusion, few if any unflanged males forced all their copulations.

Table 3 Overview of all copulations observed*:* Total number of all copulations observed during the entire study period (all-occurrence data) by male morph (unflanged and flanged) and study site (Suaq and Tuanan). Copulations were subdivided into *forced* and *unforced* copulations, whereas the *unforced* category comprised both female passive and female proceptive copulations.

		Suaq		**Tuanan**		**Total**
		Unflanged *N=32*[$]	**Flanged** *N=6*[$]	**Unflanged** *N=36*[$]	**Flanged** *N=16*[$]	
All copulations		132	32	272	46	482[£]
Forced	Female resisted	96	3	88	11	198
Unforced	Female passive	23	10	167	30	230
	Female proceptive	2	16	5	4	27

Footnotes:

[$]=The number of different males (and morphs) observed to copulate (unidentified individuals are counted as separate individuals). Note that this number does not comprise all the known males of the study site, because they may have not been observed to copulate at all.

[£]= For some copulations detailed data were missing, and they could not be attributed to a copulation type, but they are still included in the "all copulations" category. Therefore, the 3 copulation types (forced/female-resisted, passive, proceptive) may not add up to the total in the "all copulations" row.

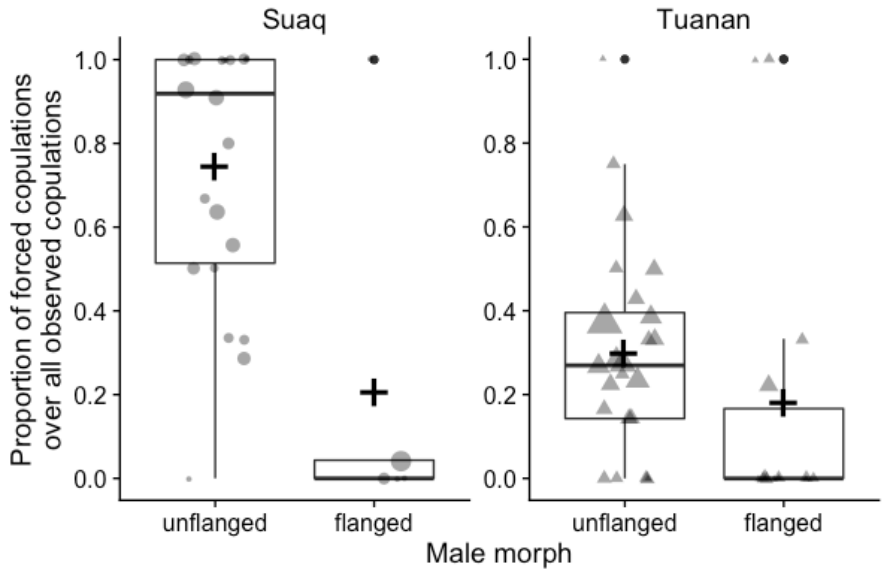
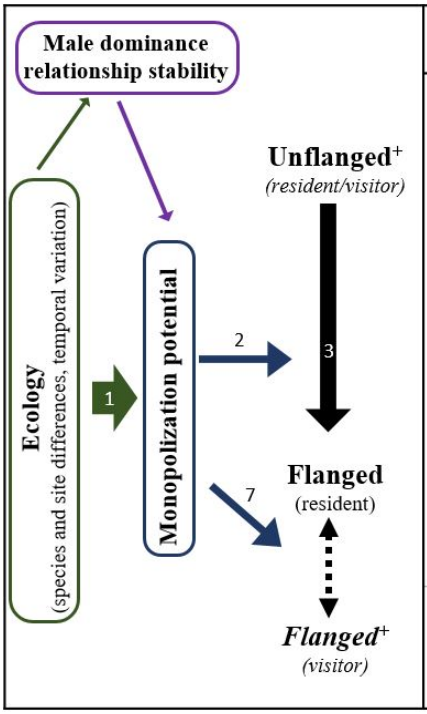


Figure 6 Proportion of forced copulations (out of all copulations observed [N=393]) by individual males (N=65) and their morph (unflanged or flanged) divided by study site (Suaq, Sumatra [*P. abelii*] and Tuanan, Kalimantan [*P. pygmaeus*]). The size of the data points is relative to the total number of observed copulations for the individual-morph data point. The boxplot is based on the median, the bold black crosses depict the mean for each morph and site. (*Note:* Only individuals of whom copulations have been observed are included in this figure).

Discussion

The extended period of male orang-utans' SSCs developmental arrest correlates with the behavioural expression of alternative reproductive tactics. Both our longitudinal and cross-sectional findings are in accordance with previous studies that have all taken a cross-sectional approach to answer similar questions about male orang-utan bimaturism (Dunkel et al., 2013; Galdikas, 1985b; Pradhan et al., 2012; Schürmann and van Hooff, 1986; Utami Atmoko et al., 2009a, 2002; Utami Atmoko and van Hooff, 2004). While flanged males are generally preferred by females, but face high costs of male-male contest competition (Dunkel et al., 2013; Spillmann, 2017), unflanged males associate and copulate far more frequently (Figure 7). The characterization of these mating tactics was heavily driven by cross-sectional analyses of Sumatran populations (*P. abelii*). Among Bornean populations (*P. pygmaeus*) where the developmental arrest of SSCs is generally shorter (Dunkel et al., 2013), previous cross-sectional studies suggested that this dichotomy was less clear-cut (Knott, 2009; Mitani, 1985a; Utami Atmoko et al., 2009a). Our findings, however, confirm for the Bornean orang-utan population at Tuanan for which we have an extensive dataset that individuals who transitioned from unflanged to flanged status exhibit a decrease in association time with females and in copulation frequency. Indeed, we found only limited evidence for study site differences, suggesting that the alternative reproductive tactics of the two morphs are generally consistent across the genus *Pongo*.

The behavioural aspect of the alternative reproductive tactics of the two male morphs and a possible scenario on how variation in developmental arrest may arise is summarized in Figure 7. We first focus on the observed behavioural patterns of unflanged and flanged males (right part of Figure 7) and discuss the morph-specific behavioural phenotypes. In the second part of the discussion, we evaluate the evolutionary aspect of developmental arrest, study site differences in this respect and temporal variation within individual and morph ("visitor" flanged male in Figure 7).



Ranging	Male-male competition	Male-female association	Preferred females	Mating
Long day journey length, larger home ranges compared to females[4]	Avoid escalated fights, tolerant to other unflanged[5] and tolerated by flanged males[6]	Frequent Prolonged association Maintain proximity to females	All, incl. nulliparous females	High copulation rate, frequently forced
Reduced[4] compared to unflanged males and flanged visitors	Long-call, confrontational assessments[7]	Rare, selective associations with receptive females, consortship[8]	Parous, receptive females	Few, selective copulations, rarely coerce
Increased compared to flanged residents[4]	*Condition-dependent confrontational assessment?*[7]	*Rare, selective associations?*	*unknown*	*Less selective? Higher coercion rate?*

Figure 7 Scheme to summarize the alternative reproductive tactics of unflanged and flanged males: The left side illustrates the mediators of orang-utan male bimaturism proposed by previous theoretical and empirical studies: Ecological variables, particularly food availability, which potentially varies between species (islands), sites (habitat) and temporally within population, determine the males' monopolization potential of females and by that mediate when flanging is beneficial. The right side summarizes the behavioural tactics of the two morphs found in both the current and previous studies. The text in *italics* indicates hypotheses that need testing in future studies.

Footnotes:

+= Reports from flanged (and unflanged) males, especially in Bornean populations, suggest that males show temporal variation in their reproductive tactics according to their condition. We added the visitor flanged males as an additional category and future studies on individual male careers will reveal if there is such temporal variation.

1: R. A. Delgado and van Schaik 2000; van Schaik 1999; Wich et al. 2011

2: Pradhan et al., 2012; Dunkel et al., 2013;

3: Dunkel et al., 2013; Marty et al., 2015;

4: Singleton and van Schaik, 2001; Morrogh-Bernard, 2009; Singleton et al., 2009; Utami and van Hooff, 2004; A.A., unpubl.data;

5: Galdikas, 1985a; Sugardjito et al., 1987; Reukauf, 2019;

6: Mitani, 1985a; Schürmann and van Hooff, 1986

7: Spillmann et al., 2017; Spillmann, 2017; Mitani, 1985b

8: Fox, 1998; Fox, 2002; Mitra Setia and van Schaik, 2007; Spillmann et al., 2010, 2017

Unflanged males associate more frequently than flanged males

Relative to flanged males, unflanged males spent more time in association with females, especially with nulliparous females, and spent a higher proportion of that association time in close proximity to females. First, because female orang-utans do not exhibit any morphological fertility advertisement (sensu Nunn, 1999), and unflanged males cannot rely on female sexual proceptivity (Fox, 1998; Knott et al., 2010), associations and close proximity to females may enable unflanged males to monitor females' reproductive status and sexual activities. Being tolerated at distance by flanged males (Mitani, 1985a; Schürmann and van Hooff, 1986) and their relatively high tolerance towards each other (Galdikas, 1985b; Sugardjito et al., 1987) allows unflanged males to avoid the high costs of male-male competition and potentially to eavesdrop on female (proceptive) sexual behaviour towards other males during prolonged associations. Second, unflanged male sociality may also serve to establish long-term relationships with females (Mitra Setia et al., 2009; Utami Atmoko et al., 2009a), which may eventually lead to a higher reproductive success. The increased association time with nulliparous females in our

study could point into the direction of both an increased siring success with nulliparous females (Utami Atmoko et al., 2002) and the establishment of long-term relationships. Third, unflanged male sociality may also assist social and ecological skill development after dispersal (Nater et al., 2011; Mörchen et al., in prep.). To fully understand how unflanged males benefit from sociality, and the extent to which this sociality is a mating tactic and relates to siring success, future studies are needed. For now, we conclude that the higher association frequency of unflanged males may be representative of their "*best-of-a-bad-job*" mating strategy.

Flanged males are more selective in when to associate and with whom (Figure 7), and are only involved in long associations with females around conception (Fox, 1998; Schürmann and van Hooff, 1986; Utami Atmoko et al., 2009a), likely because they incur higher costs from associating with females (JK, unpubl.data) and can rely on female choice (Fox, 1998; Knott et al., 2010). This was also supported by the current results: Both flanged males (Wodan [Tuanan], Islo [Suaq]), who had exceedingly high association rates, were involved in prolonged consortships around the time that these females conceived. Two flanged males which transitioned from unflanged to flanged status at Suaq (Xenix and Balu) did not show a decrease in proximity to females during associations (Figure 5), which can be explained by the presence of a fertile female during the observation periods. In conclusion, flanged males associate selectively, preferably with parous females, when females are likely fertile and thus, their selective, long associations clearly indicate mating effort.

Unflanged males are notoriously understudied relative to both flanged males and adult females with their dependent offspring. Even at our study sites, focal follow data of unflanged males, especially in the Suaq population, are very limited. Likely due to this limitation we could not find any significant difference in unflanged males' sociability with females (number of females in association based on full-day focal follows) between Tuanan and Suaq. This site difference was found for the sociability (average daily party size) of parous females (Mitra Setia et al., 2009), for whom more focal data are available than for unflanged males. Because unflanged males were often encountered and the focal follow started on days when they were in association with a female (Suaq: 39±SE 8% and Tuanan: 40 ±SE 4% of first day focal follows with a female associate), the focal follow data may be skewed towards higher association frequencies for unflanged males. Flanged males were regularly located by researchers due to their long calls or conspicuous travel and less when in association with females (Suaq: 33±SE 6% and Tuanan: 15±SE 2% of first day focal follows with a female associate). However, such a bias cannot explain the lack of site differences. For now, we infer that unflanged males are less sensitive to costs of association than females (and flanged males) at Tuanan, despite its lower productivity (Wich et al., 2011), because of the benefits they gain from associating with females (chapter 3).

Ranging and female encounter rates

Previous studies have established that unflanged males travel more and farther each day than flanged males (Morrogh-Bernard et al. 2009; Singleton et al. 2009; van Schaik et al. 2009; A.A. unpubl. data). Thus, their smaller body size and higher mobility gives unflanged males an advantage over the larger-bodied flanged males to find and associate with females (Utami Atmoko and van Hooff, 2004). Flanged males were reported to rely on receptive females to actively approach their long-calls (Fox, 2002; Mitra Setia and van Schaik, 2007), which would enable them to be selective when to associate with females, but also attracts competitors (Mitani, 1985b; Spillmann et al., 2017).

The "call-and-wait" strategy of flanged males is, however, heavily based on research in West Sumatran populations. The situation on Borneo is less clear. First, evidence for a female-attracting function of the long-call remains scarce for Bornean sites (Mitani, 1985b; Spillmann et al., 2010), although this could reflect small sample sizes. Second, long-call rates and confrontational assessment among flanged males increased during periods when females were fertile at Tuanan (Spillmann et al.,

2017), unlike in Suaq on Sumatra, suggesting that male-male competition increases only during selected periods. Third, flanged males at Bornean sites may encounter females more frequently because of their higher mobility due to ground travel (Ashbury et al., 2015). In populations where ground travel is common, flanged males may range further to encounter females without emitting long-calls which attract potential competitors (Mitani, 1985b). Finally, individual flanged males may show more temporal variation in their physiological condition and accordingly, mating tactics, as indicated in figure 7 by the resident and visitor flanged male strategy. Future studies are therefore needed to establish if in Bornean populations i) ground travel by flanged males leads to higher female encounter rates and ii) flanged males can rely on receptive females approaching their long calls.

Unflanged males copulate more frequently than flanged males

Unflanged males showed a higher copulation frequency than flanged males. The within-individual change of copulation frequency after males developed their SSCs convincingly emphasizes the switch in male mating tactics. The higher copulation numbers of unflanged males are not just the result of increased association time with females, as the difference between male morphs remained even when controlling for association time with females. One possible explanation for their lower copulation rates is that flanged males, with their larger body size, may incur higher energetic costs from mating than unflanged males. Our results rather suggest that it is the interaction between male and female mating tactics: female proceptive behaviour towards preferred flanged males, which occurs primarily around the time of conception (Fox, 1998; Knott et al., 2010), may contribute to lower copulation rates for flanged males. Unflanged males generally receive less female proceptive behaviour and may therefore initiate mating during periods when females are less likely to be fertile (chapter 4). The exceedingly high copulation (and association) rates of the dominant flanged male at Suaq not only reflect the high monopolization potential of the dominant flanged male at Suaq compared to flanged males in Tuanan who have less stable presence and dominance relationships (Dunkel et al., 2013; Spillmann et al., 2017), but also further emphasize the interplay between male and female mating tactics.

Unflanged males force copulations more frequently than flanged males

Even though unflanged males forced a higher proportion of their copulations than flanged males, sexual coercion is not an "unflanged-male-default". Indeed, the data indicate that it rather is a variable male mating tactic. The coercion rate among different males was highly variable (Figure 6), and most unflanged males were observed to have both unforced and forced copulations. Because forced copulations are the result of both male and female mating tactics (Emery-Thompson and Alvarado, 2012), the question arises when male and female interests collide. Knott et al. (2010) suggest that female preference, both positive and negative, changes with reproductive state. Furthermore, the increased proportion of forced copulation in the Suaq population compared to Tuanan points to a more pronounced female aversion to unflanged males at Suaq than at Tuanan. Nevertheless, it is important to note the limited observation hours of unflanged males in the Suaq population compared to Tuanan.

Contrary to both our prediction and previous studies, we found only limited evidence for higher coercion rates among flanged males at Tuanan compared to Suaq. Even though there is evidence for more direct contest competition among flanged males at Tuanan than at Suaq (injuries resulting from physical fights: Dunkel et al., 2013; long call confrontational assessment: Spillmann et al., 2017), individual flanged males at Tuanan were not more likely to force copulations (N=6 of 38 total copulations observed) than at Suaq (N=2 of 31 total copulations). First, this may be an artefact of the flanged males rarely copulating overall and therefore being less likely to encounter female resistance. Second, we only included copulations of identified flanged males from both sites. This meant that half of all forced copulations (5 of 11) at Tuanan and one third (1 of 3) at Suaq, which were committed by unidentified flanged males, were excluded from the analyses (Table 3). Previous studies looked at

average rates of forced to unforced copulations over many different males and lumped individuals together (Knott, 2009; Utami Atmoko et al., 2009a; Utami Atmoko and van Hooff, 2004). The fact that unknown flanged males encounter more female resistance may be informative in itself, since they were presumably visitors to the study area (sensu Spillmann 2017) (Figure 7). If there is a risk of infanticide in orang-utans (Knott et al. 2010; Scott et al. 2019; but see Beaudrot et al. 2009), females may be more reluctant to mate with visitor (or subordinate) males (sensu Dunkel et al., 2013), as this may reduce the paternity certainty of eavesdropping resident males. Third, the Suaq orang-utan population has had a period of instability from 2014 to 2018, when the former dominant flanged male, Islo, was wounded but no immediate successor was apparent (C. Schuppli, unpubl. data). In our sample, Islo was still an outlier with high association and copulation frequencies and low coercion rates, confirming previous studies with extremely low copulation rates, and hence no forced mating, by dominant flanged males (Fox 2002). However, like in other studies, we also took averages over individual and morph and did not account for temporal variation in within-morph mating tactics, as was suggested in previous work (Spillmann, 2017). Due to long absences of certain males from the study area (Utami Atmoko et al., 2009b), it remains difficult to capture such temporal variability.

Variation in male morph specific tactics

Although there is a clear distinction between unflanged and flanged males with respect to their copulation frequency and their coercive tendencies, reports on coercion rates and mating and reproductive success of the two morphs are highly variable, both within and between study sites (reviews: Knott, 2009; Utami Atmoko et al., 2009). This spatio-temporal variability may partly reflect small sample sizes and the fact that individuals had to be lumped for analyses, but does not appear to be linked to one particular cause. Thus, multiple factors, particularly ecology and male dominance relationship stability (Figure 7), may play a role in shaping both male and female reproductive tactics in orang-utans. More fine-grained analyses on the temporal variability of individual males' behaviour and physiological condition and female preferences (Fox, 2002; Spillmann et al., 2017, 2010; Utami Atmoko et al., 2009a, 2002; Utami Atmoko and Setia, 1995), especially in populations with a less pronounced developmental arrest, are needed to gain further insights into the dynamics and variability of the delayed development of SSCs in orang-utans.

In populations with high monopolization potential, i.e. low costs of association, and the long-term presence of a dominant flanged male, there may be more pronounced female preferences and, ultimately, a higher reproductive skew. Such a pattern has mostly been reported in West Sumatran populations (Fox, 1998, Suaq: 2002; Ketambe: Mitra Setia and van Schaik, 2007; Schürmann and van Hooff, 1986). The unstable periods in between the tenure of these dominant males may result in different mating patterns and a lower reproductive skew (Utami Atmoko et al., 2009a, Ketambe: 2002; Utami Atmoko and Setia, 1995). Bornean populations have generally been characterized by less pronounced dominance and more frequent confrontational assessment (Galdikas, 1985a; Mitani, 1985b; Spillmann et al., 2017). Correspondingly, the reproductive skew was hypothesized to be lower because of the lower monopolization potential (Pradhan et al., 2012), though with paternities still largely concentrated among flanged males (Dunkel et al., 2013; Goossens et al., 2006). However, high reproductive skews concentrated on a single flanged male have been reported for two Bornean populations, both of which were provisioned at designated, centralized feeding platforms (Banes et al., 2015; Tajima et al., 2018). These results can thus be taken as a natural experiment, where food is no longer the limiting factor for associations (Galdikas, 1988; van Schaik, 1999), allowing dominant flanged males to decrease their home range sizes and increase their association time, as seen in West Sumatran populations (Suaq: Singleton and van Schaik, 2001). Thus, when the energetic costs of association are not prohibitively high, Bornean flanged males can also monopolize reproductive access to females (Figure 7).

To fully understand the ultimate function of the observed variability of the developmental arrest of SSCs among orang-utans, we need to have more data on the paternity allocation in different study populations, along with long-term behavioural data, especially relating to fluctuations in male dominance (Dunkel et al., 2013; Utami Atmoko et al., 2009a; Utami Atmoko and Setia, 1995). From an evolutionary point of view, the prolonged unflanged period in Sumatran populations, or populations with high monopolization potential in general, may be explained by their higher siring success (reflecting their more active travel and higher rates of encountering females) compared to subordinate flanged males (whose travel is energetically costly and less likely to result in encountering females, and who cannot afford to long call) (Dunkel et al., 2013). This is further supported by the more frequent resistance behaviour of females, i.e. negative female choice, towards unflanged males at Suaq than at Tuanan.

Conclusion and implications

Orang-utans are unique among primates in that they exhibit irreversible bimaturism combined with an extended period of developmental arrest. Pradhan et al. (2012) explained this phenomenon by the high monopolization potential of the dominant male combined with some opportunities for fertilization by unflanged males. In sum, unflanged males follow a "best-of-a-bad-job" tactic (Dawkins, 1980): they avoid direct male-male competition, but are not preferred by females. In other primate species, male SSCs, which may function as ornaments for female choice (Grueter et al., 2015; Lüpold et al., 2019; Pradhan and van Schaik, 2009), may be delayed in their development relative to the timing of the onset of sexual maturity. However, because these traits often comprise colouration or other reversible phenotypes (vervet monkeys: Gerald et al., 2010; Verreaux's sifaka Lewis and van Schaik, 2007; mandrills: Setchell, 2005), the costs of developing such SSCs are lower and can be reversed to some extent, as opposed to flanging in orang-utans.

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Chapter 3: The Cost of Association with Males for Bornean and Sumatran Female Orang-utans – a hidden form of sexual conflict?

Julia A. Kunz[1], Guilhem J. Duvot, Maria A. van Noordwijk[1], Erik P. Willems[1], Manuela Townsend[1], Neneng Mardianah[2], Sri Suci Utami Atmoko[2], Erin R. Vogel[3], Taufiq Purna Nugraha[4,5], Michael Heistermann[6], Muhammad Agil[5], Tony Weingrill[1], Carel P. van Schaik[1]

1) Department of Anthropology, University of Zurich, Switzerland
2) Faculty of Biology and Primates Research Center Universitas Nasional, Indonesia
3) Department of Anthropology, Rutgers The State University of New Jersey, USA
4) Research Center for Biology, Indonesian Institute of Sciences (LIPI), Cibinong, Indonesia
5) Agricultural University Bogor, IPB, Indonesia
6) Endocrinology Laboratory, German Primate Center, Leibniz-Institute for Primate Research, Germany

Abstract

Socioecological theory predicts a trade-off between the benefits of sociality and the ecological costs of increased feeding competition. Orang-utans' semi-solitary lifestyle has been attributed to such high costs of association and the low predation risk. Because orang-utan females do not advertise fertility with any morphological indicator (e.g. sexual swellings), they are vulnerable to sexual coercion by males over an extended period. Sexual coercion, in the form of forced copulations, is relatively frequently observed and generally associated with the large sexual dimorphism and the semi-solitary lifestyle. However, male and female interests may not only conflict about mating, but also about association maintenance. Males may benefit from associations with females to monitor their reproductive state and attempt to monopolize their sexual activities, while females incur ecological costs. Here we evaluate association costs for two different species of female orang-utans with both males and females at two study sites: Suaq, Sumatra (*Pongo abelii*) and Tuanan, Borneo (*Pongo pygmaeus wurmbii*). The association frequency was higher at Suaq than at Tuanan, and accordingly, we found that the cost of association, in terms of reduced feeding to moving ratio and increased time being active, are higher in the less sociable population of Tuanan. Moreover, prolonged associations with males led to increased female faecal cortisol metabolite (FCM) levels at Tuanan. Accordingly, males generally initiate and maintain such costly associations with females. We conclude that male-maintained associations are an expression of sexual conflict in orang-utans, at least at Tuanan. This high cost of association to orang-utan females may be responsible for the lack of sexual signalling, while needing to confuse paternity.

Keywords: concealed ovulation, cost-of-sexual-attraction hypothesis, faecal cortisol, socio-ecology, sexual coercion

Introduction

In most mammals, female reproductive success is limited by access to food resources, while that of males is limited by access to females (Darwin, 1871; Emlen and Oring, 1977). Hence, males and females have different behavioural strategies to optimize their lifetime fitness, which may lead to sexual conflict (Parker, 1979; Trivers, 1972). In species with long lactational infertility and no paternal care, sexual conflict is likely to be more pronounced due to high male-biased operational sex ratio (van Schaik, 2016). One promising example of such species is the orang-utan, where females exhibit the longest inter-birth intervals in primates of 6 to 9 years (van Noordwijk et al., 2018), and males do not provide direct paternal care for infants (Rijksen, 1978; Utami Atmoko et al., 2009a). Hence, male-male competition for receptive females is high, which carries a high potential for sexual conflict (Trivers, 1972). However, the relative importance of male-male competition, female choice and sexual conflict in respect to the orang-utan mating system remains incompletely understood (Fox, 1998, 2002; Knott, 2009; Knott et al., 2010; Nadler, 1981; Spillmann et al., 2010, 2017; Utami Atmoko et al., 2009a). There is evidence though for behavioural expression of sexual conflict, in the form of forced copulations, which is frequently observed in orang-utans (Galdikas, 1985a; Knott et al., 2010; Mitani, 1985a; Schürmann and van Hooff, 1986). Females are vulnerable to this form of sexual coercion because of the pronounced sexual dimorphism (Smuts and Smuts, 1993), the semi-solitary lifestyle (Rijksen, 1978; females spend about 50-80% alone, only with their [semi-]depdendent offspring [van Schaik, 1999; van Noordwijk et al., 2009]) and the absence of morphological fertility advertisements, such as sexual swellings (Nunn, 1999; Zinner et al., 2004). Interestingly, apparent physical injuries resulting from forced copulations have not been reported, and males seem to use only as much force that is necessary to achieve intromission (Knott, 2009).

Sexual conflict over associations

Sexual conflict may not only arise about actual mating, but also about associations. Female orang-utans are at the extreme solitary end of the fission-fusion spectrum (van Schaik, 1999). The low association frequency (van Schaik, 1999) suggests that the costs of associations, in terms of increased scramble feeding competition, are likely substantial for both males and females (Galdikas, 1988; Utami Atmoko et al., 1997; van Schaik and Fox, 1996). For adult females, these costs likely are centred around energy acquisition, while for males the costs could include the risk of aggression from other males and energy acquisition. Yet, associations may occur nevertheless, even if only one partner benefits. Specifically, because of the rare siring opportunities, male association decisions may be less cost sensitive (van Schaik, 1999), and males may accept foraging costs due to increased copulation opportunities (chimpanzees: Emery-Thompson and Georgiev, 2014; Georgiev et al., 2014; orang-utans: Mitani, 1989). Therefore, non-preferred males likely benefit from associations with females, as this presumably facilitates monitoring their reproductive status and sexual activities, also when females are unlikely to be fertile. As a result, females and males may conflict in their interest to associate with each other (Parker, 1979; Trivers, 1972). In fact, males often attempt to prevent females from leaving associations (van Noordwijk and van Schaik, 2009). Thus, while male orang-utans may benefit from associating with females, females may attempt to reduce time spent in associations because of potential foraging costs. If this is indeed the case, male-female association in orang-utans can be considered an expression of sexual conflict.

Absence of fertility advertisement and the cost-of-sexual-attraction hypothesis

Female orang-utans do not exhibit any apparent graded, morphological signals advertising fertility (e.g. sexual swellings: Nunn, 1999; Zinner et al., 2004). Although rare observations of female proceptive copulations with dominant males have been linked to the peri-ovulatory period (Fox, 1998; Knott et al., 2010), ovulation appears largely concealed, as males initiate copulations independent of the

females' reproductive state and during periods of lactational infertility (Knott et al., 2010; Nadler, 1981; chapter 4). Unpredictable ovulation in other catarrhine primates has been linked to the need to counteract male monopolization and serves as a paternity confusion strategy to offset the risk of infanticide (Hrdy, 1979; van Noordwijk and van Schaik, 2000; van Schaik et al., 2000, 2004).

However, especially semi-solitary females may be ecologically constrained by increased scramble competition costs of grouping to signal prolonged fertility to males and thus, achieve such paternity confusion. Wrangham (2002) suggested that females of the genus *Pan* may be ecologically constrained in their oestrus length and mating rate because of the potentially high costs of association while needing to counteract the risk of sexual coercion. The 'cost-of-sexual-attraction' hypothesis (Wrangham, 2002) offers one explanation for the variation in fertility advertisement in fission-fusion systems. Accordingly, the cost of association for females in the genus *Pan* i) negatively correlates with the number of swelling cycles to conception (Deschner et al., 2003; Deschner and Boesch, 2007; Douglas et al., 2016; Emery-Thompson, 2005) and, ii) positively correlates with the rate of sexual coercion. Bonobos (*Pan paniscus*) are at the low cost of association end (Nurmi et al., 2018), have very prolonged periods of sexual attractivity (Douglas et al., 2016), and sexual coercion by males is virtually absent (Hohmann et al., 2019; Paoli, 2009). The costs of association for chimpanzee females varies geographically. In the more gregarious Western chimpanzees (*P. troglodytes verus:* Boesch and Boesch-Achermann, 2000; Riedel et al., 2011), rates of sexual coercion are low (Stumpf and Boesch, 2010) and females may even directly profit from prolonged sexual attractiveness by obtaining increased support from males in food contests as their swelling size increases (*Social Passport Hypothesis*: Deschner and Boesch, 2007). In contrast, in Eastern chimpanzees (*P. troglodytes schweinfurthii)*, females' foraging effort is compromised and their energy balance negative with an increasing number of males in association (Emery-Thompson et al., 2014). Especially low-ranking females exhibit elevated faecal cortisol levels with increasing sub-group size, particularly with an increasing number of males in association (Markham et al., 2014). Sexual coercion by males is frequently reported in Eastern chimpanzees (Muller et al., 2011, 2007) and cycling females exhibit elevated urinary cortisol values on days after they received male aggression (Emery-Thompson et al., 2010). In sum, in a high-quality habitat both the immediate and delayed benefits to associate with males and to signal fertility over an extended period may outweigh the costs for females. Following the 'cost-of-sexual-attraction' hypothesis, the absence of morphological fertility advertisement in the genus *Pongo* may be explained by the prohibitively high costs of association, which we set out to evaluate here.

Geographic variation in sociability in orang-utans

In the absence of high predation pressure due to the arboreal lifestyle (van Schaik and van Hooff, 1983), food abundance is the major constraint to population density and sociality in orang-utan (Hardus et al., 2013; van Schaik, 1999; Vogel et al., 2015). Fruit availability is not only correlated with, and probably responsible for, the higher association frequency in Sumatran (*Pongo abelii*) (average party size ranging from 1.6 to 1.9) compared to Bornean orang-utans (*Pongo pygmaeus*) (average party size ranging from 1.05 to 1.3) (Mitra Setia et al., 2009; van Schaik, 1999; Wich et al., 2011), it also likely constrains associations within populations over time (Fox, 1998; van Schaik and Fox, 1996; Wich et al., 2006; Meric de Bellefon et al., in prep.). A high degree of scramble competition has been held responsible for the low female sociability and evidence for direct female-female contest competition has been reported (Knott et al., 2008; Marzec et al., 2016; Utami Atmoko et al., 1997; van Noordwijk et al., 2012). The ecological effect on association frequency, however, would be expected to be most prominent in associations between males and females because of their different ranging patterns and activity budgets connected to their distinct energetic demands (Harrison et al., 2010; Morrogh-Bernard et al., 2009; van Schaik et al., 2009b; Vogel et al., 2017). In previous studies, it has been shown that day journey length increases with increasing association size, as a result of increased scramble competition both in Sumatran and Bornean populations (Fox, 1998; van Schaik, 1999; Wartmann et al., 2010).

In some respects, it seems that the two orang-utan species have adapted to their distinct conditions, and even under similar food availability in captivity they show a different response to increased sociability. In zoos, Bornean orang-utans (*P. pygmaeus*) permanently housed with up to 5 adults exhibited overall higher faecal cortisol metabolite (FCM) levels than the more gregarious Sumatran orang-utans (*P. abelii*) living in groups with up to 8 adults, which was attributed to species differences in the sensitivity to social stress (Weingrill et al., 2011). This finding is further supported by the lower FCM levels in captive Bornean orang-utans that were kept in fission-fusion like housing systems than the ones kept in a stable group (Amrein et al., 2014). Taken together, these results suggest that social factors, especially extended sociality, lead to a stronger physiological stress response in the less sociable Bornean orang-utans, suggesting that they will prefer lower association rates also in the wild.

Male bimaturism and sexual conflict

Orang-utans exhibit a uniquely pronounced male bimaturism, which has been associated with alternative male reproductive strategies (Dunkel et al., 2013; MacKinnon, 1974; Pradhan et al., 2012; Utami Atmoko and van Hooff, 2004). Unflanged males, who lack secondary sexual characteristics, reportedly associate, copulate and coerce copulations more frequently than flanged males (Galdikas, 1985b; Knott, 2009; MacKinnon, 1974; Mitra Setia et al., 2009; Sugardjito et al., 1987; Utami Atmoko et al., 2009a; chapter 2). Flanged males, who have fully developed secondary sexual characteristics, emit long calls and were reported to rely largely on female choice around conception (Fox, 2002; Mitra Setia and van Schaik, 2007; Spillmann et al., 2010). Although there is evidence for variation among populations and species in these male morph reproductive strategies (Delgado and van Schaik, 2000; Knott and Kahlenberg, 2007; Mitra Setia and van Schaik, 2007; Spillmann et al., 2017; Utami Atmoko et al., 2009a), sexual conflict over associations is likely more pronounced with unflanged males than with flanged males.

Aim of the study

Associations and their maintenance may present another, more subtle, context of sexual conflict in addition to forced copulations in orang-utans. Following the 'cost-of-sexual-attraction' hypothesis (Wrangham, 2002), high costs of association may be responsible for the absence of morphological fertility advertisements in female orang-utans and thus, make them vulnerable to sexual coercion, as males may not have accurate cues of female reproductive status. Here we evaluate the costs of association for female orang-utans with both females and males at two study sites, Suaq (*P. abelii,* Sumatra) and Tuanan (*P. pygmaeus,* Borneo) using behavioural and endocrine data. We refer to study site rather than species differences, although we cannot exclude that these translate to species differences, we do not have information on within species variability as we evaluate only one study site per species. We included female-female associations as a comparative category with the assumption that females have similar incentives to associate with each other (van Noordwijk et al., 2012) as opposed to male-female associations. Behavioural changes (i.e., changes in the daily activity budget) and variation in faecal FCM levels of parous females were measured in relation to different types of association and social interactions. We hypothesize that 1) females of the less sociable population, Tuanan, incur higher foraging costs, in terms of increasing moving and reduced feeding time, from associations with both males and females, 2) females may bear additional costs from agonistic interactions, especially the occurrence of forced copulations, 3) if males benefit from monitoring a female's reproductive state and potentially attempt to monopolize a female's sexual activities, they likely initiate and maintain such associations with females, 4) social interactions between males and females are rare and therefore females likely do not gain direct social benefits from associations with males (for an exception see Marzec et al., 2016), whereas associations with other females may have social benefits for their infants (e.g. play opportunities: van Noordwijk et al., 2012).

Methods

Study sites and study subjects

Behavioural focal data on individually recognized, adult females were collected at the long-term field sites of Tuanan, Mawas Reserve, Central Kalimantan, Indonesia (02°15'S; 114°44'E) and Suaq, Gunung Leuser National Park, South Aceh, Indonesia (03°02'N; 97°25'E) between July 2003 – July 2018, and June 2007 – March 2018, respectively. Because parous females are in continued association with their dependent offspring (van Noordwijk et al., 2009) and lactate over multiple years (van Noordwijk et al., 2013), both association patterns and the cost-benefit balances incurred by sociability are likely different from nulliparous (adolescent) females (Ashbury et al., in rev.; van Schaik et al. 2009). Therefore, only data on parous females with a dependent offspring were included in this study (N=20 females [Suaq: 6; Tuanan: 14]). Females, who had lost their infants due to unknown reasons (Marzec et al., 2016; Tuanan unpubl. data), were excluded from the analyses after the loss of their infants, until they had given birth to a new infant. The age of the dependent offspring of females (Table 4) was taken as a proxy for their reproductive state and included in all the analyses. Infant ages were either known, because the birth was directly observed, or estimated from the first time an infant was observed (Table 4; cf. van Noordwijk et al., 2018).

Table 4 Overview of the data available to assess the cost of association for parous females at Tuanan and Suaq.

Study Site	**Name of parous female**	**Dependent infant**		**Activity Budget**		**Hormone Samples**	
		Minimum age of infant (y)	Maximum age of infant (y)	Number of Follow Periods	Number of full-day focal follows§	Total samples available	With behavioural reference*
Suaq	Cissy	1.6	5.2	4	35	42	13
Suaq	Ellie	0.3	2.7	4	37	32	14
Suaq	Friska	0.9	4.9	8	51	33	10
Suaq	Lisa	0.5	7.7	11	77	60	15
Suaq	Raffi	0.8	1.7	1	6	12	0
Suaq	Sarabi	0.6	0.9	2	15	4	0
Tuanan	Cikipos	3.2	3.2	1	5	6	0
Tuanan	Cinta	0.9	2.7	3	17	12	5
Tuanan	Desy	0.0	5.8	13	105	54	37
Tuanan	Inul	0.1	3.3	12	77	44	24
Tuanan	Jinak	0.3	7.1	45	365	66	39
Tuanan	Juni	0.0	6.6	33	255	88	51
Tuanan	Kerry	0.0	7.5	40	280	65	38
Tuanan	Kondor	0.0	1.9	10	64	23	12
Tuanan	Milo	0.1	1.1	3	20	9	6
Tuanan	Mindy	0.1	6.9	52	390	95	65
Tuanan	Pinky	0.0	7.5	6	39	25	7
Tuanan	Sidony	0.0	6.1	6	58	45	25
Tuanan	Sumi	0.4	3.4	20	154	0	0
Tuanan	Tina	3.7	5.5	5	36	27	9

Footnotes:
* = Number of samples included in analyses
§=Number of days included in the analyses

Behavioural data

Activity budget

Behavioural data was collected according to an established, standardized protocol (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). We collected 2-min instantaneous data during full-day female focal follows on their activities (feeding, moving, resting and social interactions). We recorded all occurrences of any individual in association (within 50 metres distance) per 2-min interval and ad libitum social interactions with the focal individual. Social partners included the female's own dependent and independent offspring, adolescent individuals, adult females and males (unflanged and flanged). Although orang-utans most likely perceive the presence of other individuals at distances of more than 50 m (van Noordwijk et al., 2012, 2009), human observers on the ground usually cannot record these consistently. We subdivided social interactions into sexual, affiliative and aggressive interactions. Sexual interactions comprised genital investigations by males, copulations and copulation attempts. Copulations were labelled as either forced, if the female showed any resistance behaviour (e.g. repeated attempt to move away, struggling against the males attempt to intromit), or unforced (following the definition of Fox [1998]). Aggression (excluding forced copulations) included displays, short chases or physical aggression/fights between females and males or other females. Affiliative interactions comprised allo-grooming, touching another individual, sitting in body contact and begging for and sharing food. Because focal animals were individually recognized, we could not collect blinded data. Only data from well-trained observers with high inter-observer reliability were included in the analyses.

Association patterns and social interactions

Male focal follows collected with the same methods as the female focal follows were used to enhance the dataset on the duration of associations and a fuller record of male-female dyadic interactions resulting in 960 male-female associations (Suaq: 292; Tuanan: 668) with known start and end times. An association between two individuals could last for multiple days and contain breaks, i.e. the association partners were at a distance of more than 50 m. If breaks lasted for longer than one full-day focal follow, we considered it as two separate association units. We recorded the individual responsible for any distance changes (in distance classes: contact, no contact <2m, 2-5m, 5-10m, 10-50m) during the association, as well as the initiator (first approach to <50m) and terminator (who left to >50m) of associations. We calculated the Female Hinde Index (FHI) for female-male associations based on these approaches and leaves as follows:

$$\text{Female Hinde Index (FHI)} = \left(\frac{\text{approaches by female}}{\text{approaches by female+ approaches by male}}\right) - \left(\frac{\text{leaves by female}}{\text{leaves by female+ leaves by male}}\right)$$

A positive FHI indicates that the female was on average responsible for the maintenance of the association, while a negative FHI stands for a male-maintained association (Hinde and Atkinson, 1970). The FHIs were calculated over all known approach and leave events and distance classes per association. Detailed approach and leave data throughout the association for the FHIs is available for 638 male-female associations (Suaq: 212; Tuanan: 426).

Ecological data

The monthly Fruit Availability Index (FAI: percentage of trees with fruits over all surveyed trees) was obtained from monthly phenology surveys of ~1500 trees at Tuanan and ~1000 trees at Suaq (Harrison et al., 2010; Vogel et al., 2015). Because the FAI is generally higher at Suaq than at Tuanan (Wich et al., 2011), we z-transformed all the FAIs within study site prior to the analyses (zFAI) to assess local FAI effects rather than between site comparisons.

Endocrine data

Collection, preservation and extraction of faecal samples

To determine if associations per se and the social interactions during associations represent a physiological cost in terms of increased stress hormone output in females, we measured faecal cortisol metabolite (FCM) levels during association and non-association days. Faecal material was collected non-invasively, when individuals defecated naturally. Because there is an excretion lag time of 24-72 hours for faecal cortisol metabolites (Weingrill et al., 2011), samples were collected (preferably in the morning) on at least 5 consecutive focal follow days. Due to individual ranging patterns in orang-utans, samples could only be taken during focal follows lasting 5-10 days with at least 5 weeks between successive sample period. The methods to preserve and extract faecal samples from orang-utans for hormone analyses have been established and validated (Amrein et al., 2014; Marty et al., 2015; Nugraha et al., 2016; Weingrill et al., 2011). Because of logistic constrains and varying infrastructures at the two field sites, different preservation and extraction methods had to be used. Generally, the fresh faeces were homogenized using a stick and a 2-5 g aliquot was collected for analysis. Only samples not contaminated with urine were taken. When electricity was available and thus, a reliable freezer at the field station, the fresh faeces was collected into a polypropylene tube labelled with animal ID, date and time of collection. The samples were frozen at -18°C upon return to the field station in a solar freezer. All samples remained frozen until transported to the endocrinology laboratory at Bogor Agricultural University where samples were lyophilized, pulverized and subsequently extracted with 80% watery methanol as described in detail elsewhere (Nugraha et al., 2016; Weingrill et al., 2011). At Suaq and when electricity supply was not guaranteed at Tuanan, faecal samples were collected in the same way, but the faeces were placed in a tube containing 5 ml of 80% watery ethanol for preservation as no freezing possibilities existed at Suaq. Samples were extracted upon return to the field station by applying a field-friendly extraction method which was previously validated (Nugraha et al., 2016). Both extraction methods have been shown to produce results which are strongly correlated and do not significantly differ (Nugraha et al., 2016). Nevertheless, to control for potential extraction differences all FCM measurements were normalized within individual and method using z-transformations (van de Pol and Wright, 2009) before their use in statistical analyses.

Hormone measurement

Faecal cortisol metabolite levels were measured in a total of 745 samples (for which 370 samples with behavioural reference day) (Table 4) using a microtiter plate enzyme immunoassay (EIA) for 11ß-hydroxyetiocholanolone (Ganswindt et al., 2003), a major metabolite of cortisol in primate faeces (Heistermann et al., 2006). The assay has been previously validated and successfully applied for assessing adrenocortical activity in numerous primate species (e.g. Heistermann et al., 2006) including captive and wild orang-utans (Amrein et al., 2014; Marty et al., 2015; Weingrill et al., 2011). Samples used for this study were analysed in different cohorts at two different laboratories (German Primate Center, DPZ, and Bogor Agricultural University, IPB), with the locality of analysis for each sample included as a fixed effect in the statistical analyses (results remain the same if we standardize by both labs, method and individual, and are not shown below). EIAs were performed as previously described (Heistermann et al., 2004). Samples from the same individual were analysed on the same microtiter plate, whenever possible. Each sample was analysed in duplicate and samples with a coefficient of variation (CV) >7% between duplicates were re-measured. Moreover, any microtiter plate for which the intra-assay CV of the internal high- and low-value quality controls exceeded 10% was rerun. For the samples analysed at both IPB and DPZ, the intra-assay CVs were below 10%, and the inter-assay CVs did not exceed 15%. All FCM concentrations were expressed in ng/g dry faecal weight.

Statistical analyses

All the statistical analyses were conducted in R version 3.5.2 (R Core Team, 2018). We ran (generalized) linear mixed effect models ([G]LMM) using the 'lme4' and 'lmerTest' packages (Bates et al., 2015; Kuznetsova et al., 2017). Model assumptions (normality [for LMMs], homoscedasticity) were checked by the visual inspection of residual plots and Variance Inflation Factors were calculated to examine potential multi-collinearity issues using the 'car' package (VIF < 2, for the full model without interaction terms included and VIF < 4 for the full model with interaction terms) (Fox and Weisberg, 2018). Further, we checked all the models for influential cases and outliers (cook's distance from the package 'influence.ME' by Nieuwenhuis et al. 2012). The P value of 0.05 was used as a cut-off value for significance. For all statistical analyses, first full models including all variables (social, ecological and physiological factors) and their possible 2nd order interactions (if applicable) were set up, and compared to the control model, containing all the random and control (ecological and physiological) factors, using likelihood ratio tests.

Behavioural data – Activity budget changes

The daily activity budget was calculated from the 2-min instantaneous data taken during full-day female focal follows (N=2086; Suaq: 221; Tuanan: 1865), thus 1) it includes the association record over the entire day and 2) avoids daytime biases. Only female follow periods (FP) of at least 5 full-day focal follows (mean=8.3±SE 0.1) within 40 days (on average within 9 days) were included in the analyses to account for variation in activity budgets (van Noordwijk et al., 2012). First, we evaluated the variability of the total active time, which comprised the total hours from leaving the morning nest to entering the evening nest. Second, we evaluated if female foraging behaviour changed on days with associations and social interactions by analysing variation in daily feeding time while controlling for moving time (offset term) (henceforth referred to as F:M ratio). Daily moving hours correlate strongly with day journey length (Pearson correlation for available Tuanan data: R^2=0.76, t_{769}=32.66, P<0.0001, N=771 female full-day follows) and was therefore taken as a proxy for daily travel. We tested for the effects of social, physiological and ecological factors on active time and F:M ratio in linear mixed models. We built in the female follow period (FP) nested in female identity as random intercepts to avoid pseudo-replication. The separate analyses on the changes of all activity budget components (feeding, resting and moving hours) including separate analyses for each study site are reported in the supplementary materials.

As social factors, we included the total cumulative time spent with either males or females and any agonistic and sexual interaction recorded as fixed effects. We chose to include the daily cumulative hours spent with either adult females or males to account for multiple individuals in association and the duration spent with each of them (including both association time and the number of individuals as separate variables would have led to multi-collinearity issues). Because consecutive association days are likely inter-dependent and there may be compensatory effects, we also included the total number of (known) consecutive days in association with either males or females in the full model. We combined the occurrence of forced copulations and other male aggression to a daily male-female cumulative aggression index, coded for severity (0=no aggression; 1=aggression not directly in a sexual context and no physical contact, such as displays, chases and displacements; 2=forced sexual interactions). Days with female-female aggression were rare (N= 2 [Suaq], 16 [Tuanan]), and could only be included as presence/absence data, and not coded for the severity. Further, we controlled for potential confounding physiological (the age of the dependent offspring) and ecological factors (Fruit Availability Index [FAI]), overarching site differences (Tuanan, Suaq), and the total time spent in social interactions with any partner (including own dependent infant and association partners; social interactions account for ~0.5% of the total active time [Tuanan: 0.4%; Suaq: 1.1%]). We tested for interaction terms between study site and social factors to check for population differences. Interaction terms were only included in

the final model, if they improved the model fit based on likelihood ratio tests. Both control models – including study site, zFAI, age of the dependent offspring and total social interaction time – significantly improved the null models, containing only the random intercepts (and the offset term) (active time: $\chi^2_{4,8}$=53.76, P<0.0001; F:M ratio: $\chi^2_{4,8}$=55.46, P<0.0001). We excluded days when females fed less than 1 hour and their active time was below 6 hours because of serious health issues or lack of habituation, as these days revealed to be influential cases and the model assumptions were violated (for one context of these outliers see Marzec et al. 2016).

Behavioural data – Association patterns and maintenance

We evaluated the time (average daily hours) females spent in association with either other females, unflanged and flanged males during follow periods in separate analyses (LMM) with the study site, zFAI and the age of the dependent offspring as fixed effects. Individual identity was added as a random intercept.

We assessed when associations were male-maintained by setting up a binomial GLMM based on the FHI values (male-maintained when FHI< 0). We added study site, male morph, the age of the dependent offspring, local fruit availability (zFAI), the occurrence of copulations (both unforced and forced) and association duration as fixed effects. To account for having the same individuals in several association dyads, both female and male identity were added as crossed random intercepts.

We formulated a Cox proportional hazard mixed model (survival analysis) using the package 'coxme' (Therneau, 2018) to evaluate if male-female associations lasted over more consecutive days than female-female associations based on the female focal follow data. We used right-censored data to account for unknown association endings, because females were no longer followed despite still being in association (N=625 associations [Suaq: 61 associations with females, 53 with flanged males and 173 with unflanged males; Tuanan: 81 with females, 96 with flanged males, 161 with unflanged males] during 167 female FPs and of 21 females). We included both associations with known and unknown start times, because excluding associations with unknown start times (~40% of association dyads) would have introduced a bias against long associations in the analysis (for further details on this issue and for the results excluding associations with unknown start, see suppl. mat.). Besides the type of adult association partners (female, unflanged and flanged male), we added study site, zFAI and the age of the dependent offspring (y) as fixed effects in the model. We set contrasts for the association partner type to first compare association maintenance between male and female association partners and then the two male morphs. Further, we included the follow period nested in the female identity as random intercept to avoid pseudo-replication.

Endocrine data

The behavioural reference day corresponding to the measured FCM level was obtained by backdating 3 days from the date of collection of morning faecal samples and 2 days for samples collected after 2 pm (Amrein et al., 2014; Cadilek, 2009; Nugraha et al., 2016; Weingrill et al., 2011). If there were several faecal samples for one behavioural reference day, only the morning sample was included in the final analysis. FCM levels with the same behavioural reference day were strongly correlated (r=0.73, CI = [0.60, 0.83], P<0.0001, N=78). To control any sample hour bias, the time of sample collection (i.e. time of defecation) was included in the statistical analyses as a control factor although previous data on captive-housed animals showed no time-of-day effect (Weingrill et al., 2011). FCM levels were ln-transformed to normalize their distribution. Subsequently, the values were standardized within individual and extraction method used, to be able to assess FCM level changes caused by social and ecological stressors within individuals rather than between individuals (method described in van de Pol and Wright, 2009). Because such z-transformations may be sample-size dependent, we only

included those individuals in the analyses for which more than 10 samples and at least 5 known behavioural reference days for a given extraction method were available. The within-individual transformations were done including all available samples, including the samples without behavioural reference. The analysis included only the samples with a known behavioural reference day. The number of total samples available (per method and individual) was included in the analyses as a control factor. A linear mixed-effect model (LMM) was set up to test for the effect of social factors on female FCM levels. The same social factor categories as described in the activity budget analyses were tested. The time to sample extraction (days), the total number of days an individual was followed, the age of the dependent infant (y), an activity budget parameter (feeding proportion) and the Fruit Availability Index (FAI) were included in the full model to control for possible confounding factors leading to FCM changes. The female follow period was added as a random intercept to avoid pseudo-replication. Because the FCM levels were standardized within individual and method, these two factors were not included as random intercepts in the analysis to keep the models as parsimonious as possible. The analyses without the standardization procedure and including individual identity and extraction method as random intercepts yielded the same patterns and are reported in the supplementary materials. The control model with all the potential confounding factors did not improve the model fit of the null model containing the random intercept term only ($\chi^2_{3,12}$=6.96, P=0.64, ΔAIC=11.04).

Results

Activity budget changes

Active time

Female active time was on average 10.8±SD 1.0 hours (min 6.1 and max 13.1) without any association partners except for her dependent offspring, whereas on days with female associates it increased to 11.4±SD 1.0 hours (Suaq: 11.6±SD 0.8; Tuanan: 11.3± SD1.1) and on days with males in association (independent of association duration) to 11.4±SD 1.0 hours (Suaq: 11.5± SD 0.8; Tuanan: 11.4±SD 1.0). Accordingly, in both study populations, female active time increased significantly with increasing time in association with females (β=0.084±0.024, t=3.428, P=0.001) and with males (β=0.068±0.034, t=2.004, P=0.045) (Figure 8A+D). Moreover, at Tuanan a female's active time increased significantly more on days with copulations than at Suaq, as the significant interaction between study site and days with copulations indicates (β=0.387±0.158, t=2.444, P=0.02) (Figure 9A). Active time further increased with increasing number of consecutive days with males (β=0.056±0.024, t=2.385, P=0.02), the total time spent in social interactions with any social partner (β=0.556±0.155, t=3.587, P<0.001) and the local fruit availability (β=0.094±0.039, t=2.427, P=0.02). Interaction terms between site and any other social factors, except copulation occurrence, did not significantly improve the model fit. In sum, daily active time increased in both populations for females in associations, and at Tuanan on days with copulations, and accordingly, the model fit significantly improved when including social factors ($\chi^2_{8,15}$=50.312, P<0.001; N=2086 of 20 females and 279 FP; for the full model suppl. mat. Stable 10).

Foraging behaviour

Overall daily feeding time (F) decreased with both males and females in association, whereas moving (M) and resting time increased (Figure 8; for detailed analyses see suppl. mat. Stable 11, Stable 12). At both study sites, the F:M ratio of females decreased with increasing association time with males (β=-0.250±0.053, t=-4.698, P<0.001), whereas it decreased significantly more at Tuanan with increasing time with females in association compared to Suaq (β=-0.333±0.070, t=-4.763, P<0.001). Only consecutive days with females, but not with males, led to a further decrease in a female's daily F:M ratio (Table 5). Furthermore, on days with copulations, the F:M ratio decreased significantly more at Tuanan

than at Suaq (β=-0.630±0.246, t=-2.557, P=0.01). The full model for the F:M ratio including social factors was significantly better than the control model including ecological and physiological factors only ($\chi^2_{8,17}$=80.47, P<0.001, ΔAIC=62.47; N=2086 of 20 females and 279 FP) (Table 5). In sum, female foraging behaviour was negatively affected by associations with both females and males, with the effects being more pronounced for the Tuanan population.

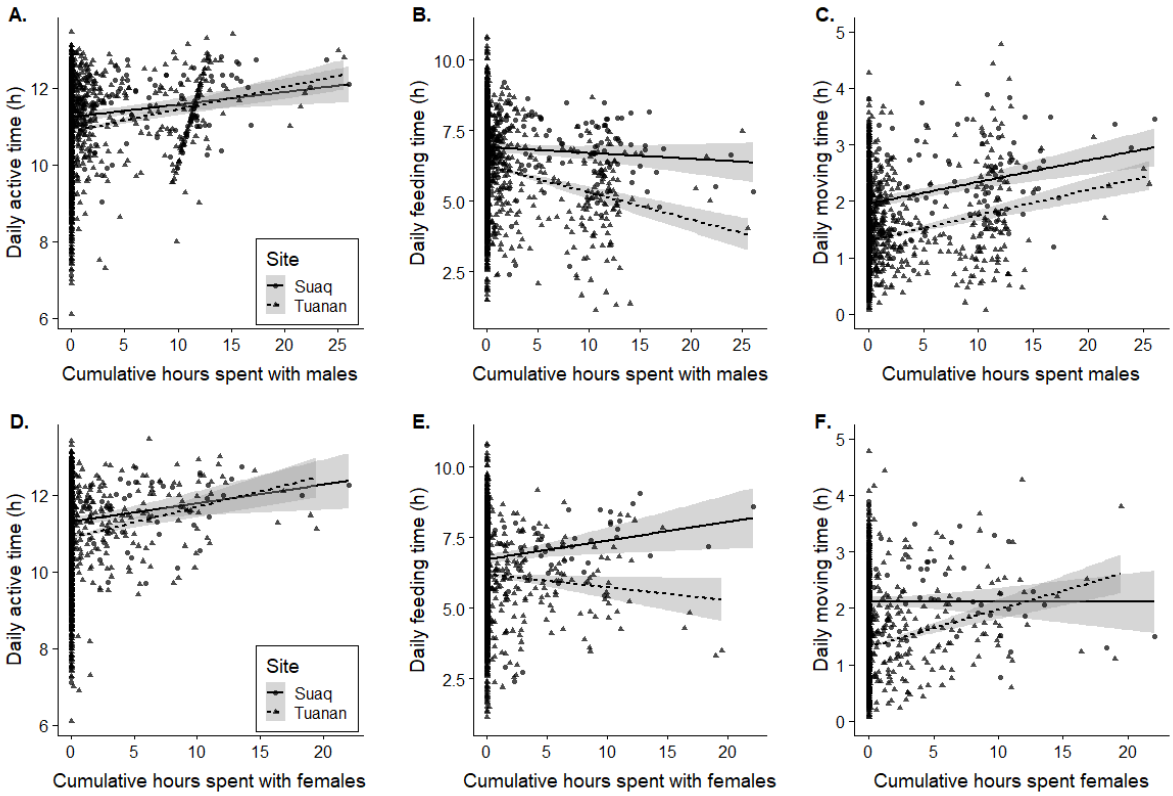

Figure 8 Daily female activity budget changes (*from left to right:* active time (A, D), feeding (B, E) and moving (C, F) hours) depending on cumulative hours spent with males (A-C) and females (D-F) and by study site (*round:* Suaq; *triangles:* Tuanan). Each data point represents one full-day focal follow (N=2095), the regression lines are the correlations between hours spent with males/females and activity hours and do not show model predictions.

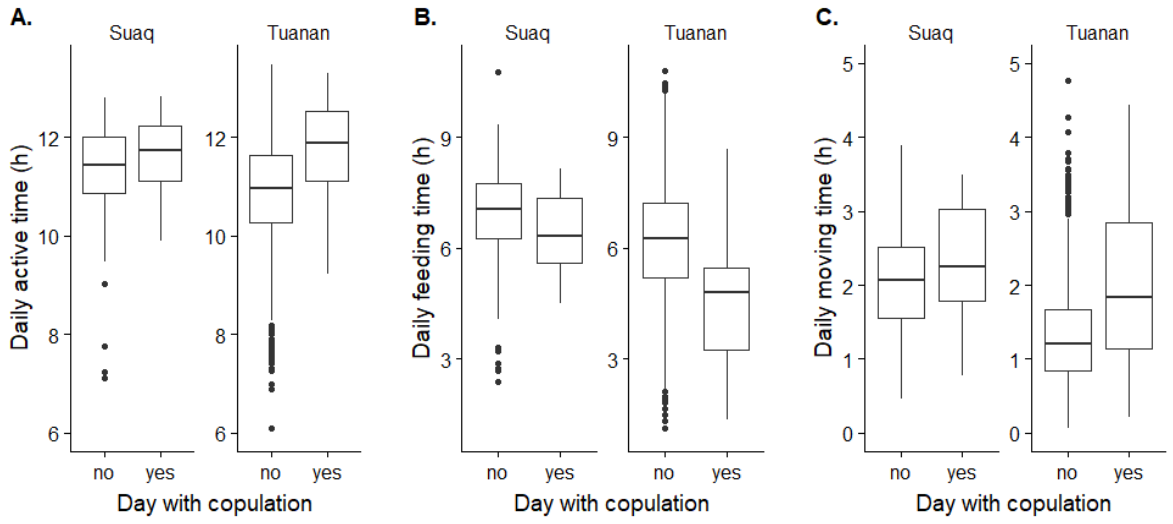

Figure 9 Daily female activity budget changes (*from left to right:* active time (A), feeding (B) and moving (C) hours) depending on the occurrence of copulations. The boxplots are based on median values of full-day focal follows (N=2095) and do not show model predictions.

Table 5 LMM output of the full model for daily feeding hours (F:M ratio) (N=2086 full-day follows of 20 parous females and 279 follow periods; $\chi^2_{8,17}$=80.47, P<0.001, ΔAIC=62.47). All fixed and control effects with P<0.05 are indicated in bold. (*Note:* z = fixed effect variable was z-transformed prior to analysis, O= offset term; C=Control factor, F= fixed effect).

		Estimate	SE	t value	P value
Intercept		4.907	0.240	-	-
Moving time (h)	*Offset*				
Site (Suaq vs. Tuanan)	C	-0.142	0.262	-	-
z Cumulative female association hours	F	0.181	0.062	-	-
z Cumulative male association hours	**F**	-0.250	0.053	**-4.698**	**<0.001**
Number of consecutive days with female	**F**	-0.167	0.070	**-2.376**	**0.018**
Number of consecutive days with male count	F	0.037	0.037	0.993	0.321
Number of copulations	F	0.193	0.206	-	-
Male-female cumulative aggression index	F	-0.052	0.140	-0.371	0.710
Female-female agonistic interactions (no vs. yes)	F	-0.549	0.312	-1.762	0.078
z Fruit Availability Index	**C**	-0.150	0.063	**-2.387**	**0.018**
z Age of dependent offspring (y)	C	-0.047	0.070	-0.678	0.498
Social interaction time (h)	**C**	-1.045	0.241	**-4.330**	**<0.001**
Site (Suaq vs. Tuanan) : z Cumulative female association hours	**F**	-0.333	0.070	**-4.763**	**<0.001**
Site (Suaq vs. Tuanan) : Number of copulations	F	-0.630	0.246	**-2.557**	**0.011**

Associations and social interactions

Association frequency

Females spent more time in association with both flanged and unflanged males as the age of their dependent offspring increased (flanged: β=0.446±0.090, t=4.944, P<0.001; unflanged: β=0.631±0.126, t=4.988, P<0.001; Stable 15; Sfigure 5), while the association time with other parous females remained constant over the age of the dependent offspring (β=0.065±0.064, t=1.019, P=0.31; Stable 15; Sfigure 5). Time spent in association with other parous females and unflanged males was generally higher at Suaq than at Tuanan (females: β=-1.063±0.357, t=-2.980, P=0.007; unflanged: β=-1.825±0.549, t=-3.323, P=0.003; Stable 15; Sfigure 5), but not with flanged males (β=0.228±0.334, t=0.682, P=0.05).

Social interactions between males and females

Affiliative social interaction occurred in 6.0±SE 0.8% of all male-female associations (Stable 16). If affiliative interactions occurred, they did so once or twice (mean 1.45±SE 0.11 occurrences) during the entire association (female-unflanged: 0.022^{-h} [interactions per association hour] [Suaq]; 0.025^{-h} [Tuanan]; female-flanged: 0.016^{-h} [Suaq]; 0.011^{-h} [Tuanan]). Male aggression towards females outside of the sexual context was observed in 7.4 ±SE 0.9 % of all dyadic male-female associations. Physical aggression by males directed at females was extremely rare (Suaq: in 1 out of 393 associations; Tuanan: 9 of 521 associations). Flanged males were significantly more likely to direct non-physical aggression towards females both at Tuanan (14.0±SE 2.2 % [0.091^{-h}]) and at Suaq (9.0±SE 2.6 % [0.025^{-h}]) than unflanged males (Tuanan: 6.6 ±SE 1.5 % [0.030^{-h}]; Suaq: 6.6 ±SE 1.5 % [0.013^{-h}]) (Stable 17). At Suaq and Tuanan both forced and unforced copulations were more frequent during associations involving unflanged (0.075^{-h} (forced: 0.052^{-h}) [Suaq]; 0.041^{-h} (forced: 0.021^{-h}) [Tuanan]) than flanged males (Suaq: 0.014^{-h} [forced: 0.011^{-h}]; Tuanan: 0.018^{-h} [forced 0.005^{-h}]) (for details on sexual interactions see chapter 4 and 5). Moreover, especially unflanged males at Tuanan frequently investigated the genitals of females during associations (female-unflanged associations: 27.4±SE 2.4% [Tuanan], 7.7±SE 1.9% [Suaq]; female-flanged associations: 1.3±SE 0.7% [Tuanan], 4.2±SE 2.1%

[Suaq]). These genital investigations occurred independent of the female's offspring age (for details see suppl. mat. Stable 18, Stable 19).

Association initiation and maintenance

Both flanged (Tuanan: 82.1%; Suaq: 73.9%) and unflanged males (Tuanan: 84.0 %; Suaq: 80.7%) initiated associations with females more frequently than the females themselves (Figure 10). Moreover, both flanged (Suaq: mean(FHI)= -0.25±SE 0.06 [N=63 associations]; Tuanan: -0.37±SE 0.04 [N=198]) and unflanged males (Suaq: -0.15±SE 0.03 [N=149]; Tuanan: -0.11±SE 0.03 [N=228]) maintained these associations (Figure 11). The full model for the probability that associations were male-maintained explained significantly more variability than the null model ($\chi^2_{3,9}$=41.27, P<0.0001, N=638 of 30 female and 139 male identities). Especially long associations were more likely male-maintained (β=1.052±0.253, OR=2.86, z=4.157, P<0.001). Association maintenance by males was independent of the female's dependent offspring age (β=0.130±0.144, OR=1.14, z=0.904, P=0.37), the local zFAI (β=-0.012±0.090, OR=0.99, z=-0.134, P=0.89) and the occurrence of sexual interactions (β=0.514±0.300, OR=1.67, z=1.709, P=0.09). Associations with flanged males were more likely male-maintained than with unflanged males (β=0.617±0.204, OR=1.85, z=3.022, P=0.003), whereas there was a trend that this difference between male morphs was more pronounced at Tuanan than at Suaq. The interaction between male morph and site tended to increase the model fit ($\chi^2_{9,10}$=3.31, P=0.07).

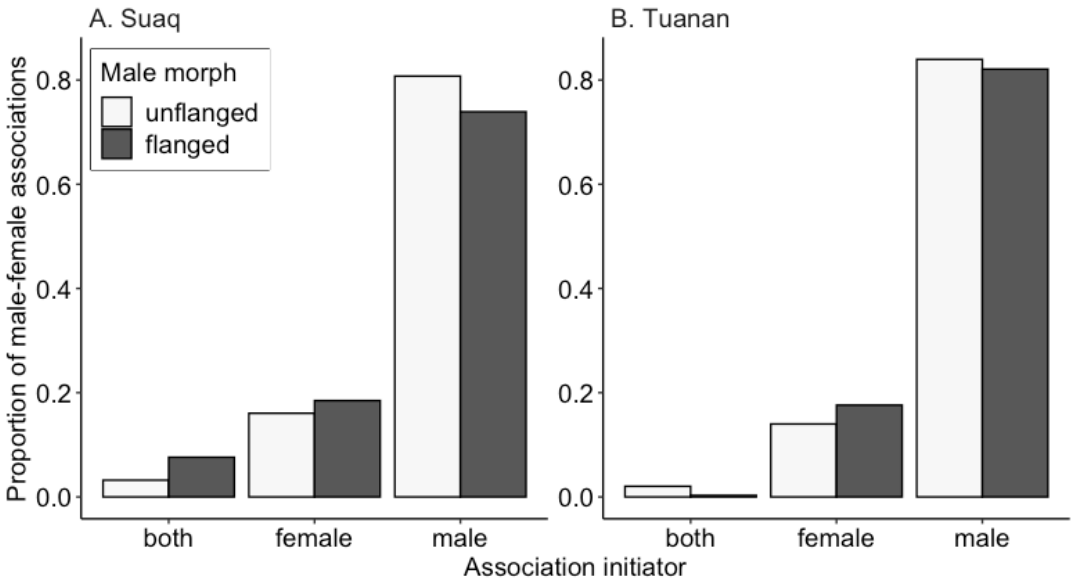

Figure 10 Proportion of association initiations by either both, female or male by study site (A: Suaq; B: Tuanan) and male morph. Only associations with a known initiator are included (N=957 [Suaq: 279; Tuanan: 678]).

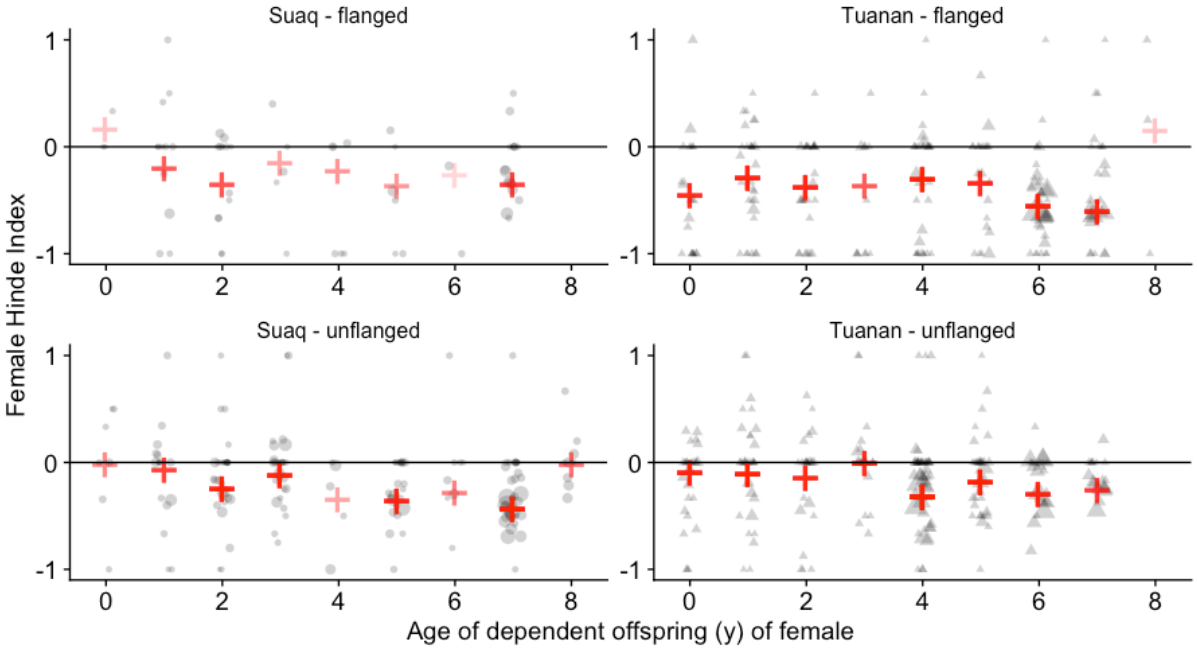

Figure 11 Female Hinde Index of associations with flanged males (left) und unflanged males (right) by study site (Suaq: top; Tuanan: bottom) by the age of the dependent offspring (y), as a proxy for female reproductive status. The red crosses indicate the weighted mean FHI (by the number of known approaches and leaves) and their transparency is relative to the number of associations included. Data points (grey) represent individual associations and only include known approaches and leaves (N=665). The data point size is relative to the association duration and a horizontal jitter function was applied to the data points to make overlapping data points more visible.

Association maintenance over multiple days

Male-female associations were maintained over more consecutive days at Tuanan (maximum 8 days) than female-female associations (maximum 4 days), whereas at Suaq this difference between the maintenance of male-female (maximum 11 days) and female-female (maximum 7 days) associations was less pronounced (Figure 12; Table 6). Accordingly, the survival analysis on the probability of ending an association was significantly better when including the interaction between study site and partner type (β= -0.234±0.089, HR=0.792, P=0.009): Female-female associations were ended faster at Tuanan than male-female associations, whereas at Suaq this difference was less pronounced (Figure 12). We could not find any difference in association maintenance probability between the two male morphs (unflanged vs. flanged) (Table 6). Associations were maintained over more consecutive days with the increasing age of the dependent offspring of a female (β=-0.169±0.066, HR=0.844, P=0.009). The interaction between the age of the dependent infant and partner type did no improve the model fit (χ^2_2=0.83, P=0.66). Local zFAI did not have an effect on the association maintenance (Table 6).

Table 6 Probability of ending an association: Output of the Cox proportional hazard mixed model for the total number of (known) days in association by the type of association partner, study site, age of the dependent offspring (y), and zFAI (χ^2_7=28.80, P=0.0002, N=625 associations of which 426 with known end, of 21 female identities and 167 FPs).

	β	SE	Hazard ratio	z value	P value
Site (Suaq vs. Tuanan)	0.554	0.146	1.74	-	-
Association partner					
Sex (male vs. female)	0.233	0.071	1.26	-	-
Male morph (unflanged vs. flanged)	-0.029	0.103	0.97	-	-
Age of dependent offspring (y)	-0.169	0.066	0.84	**-2.560**	**0.010**
zFAI	-0.021	0.067	0.98	-0.310	0.760
Site : Association partner sex (male vs. female)	-0.234	0.089	0.79	**-2.620**	**0.009**
Site : Partner male morph (unflanged vs. flanged)	-0.019	0.130	0.98	-0.140	0.890

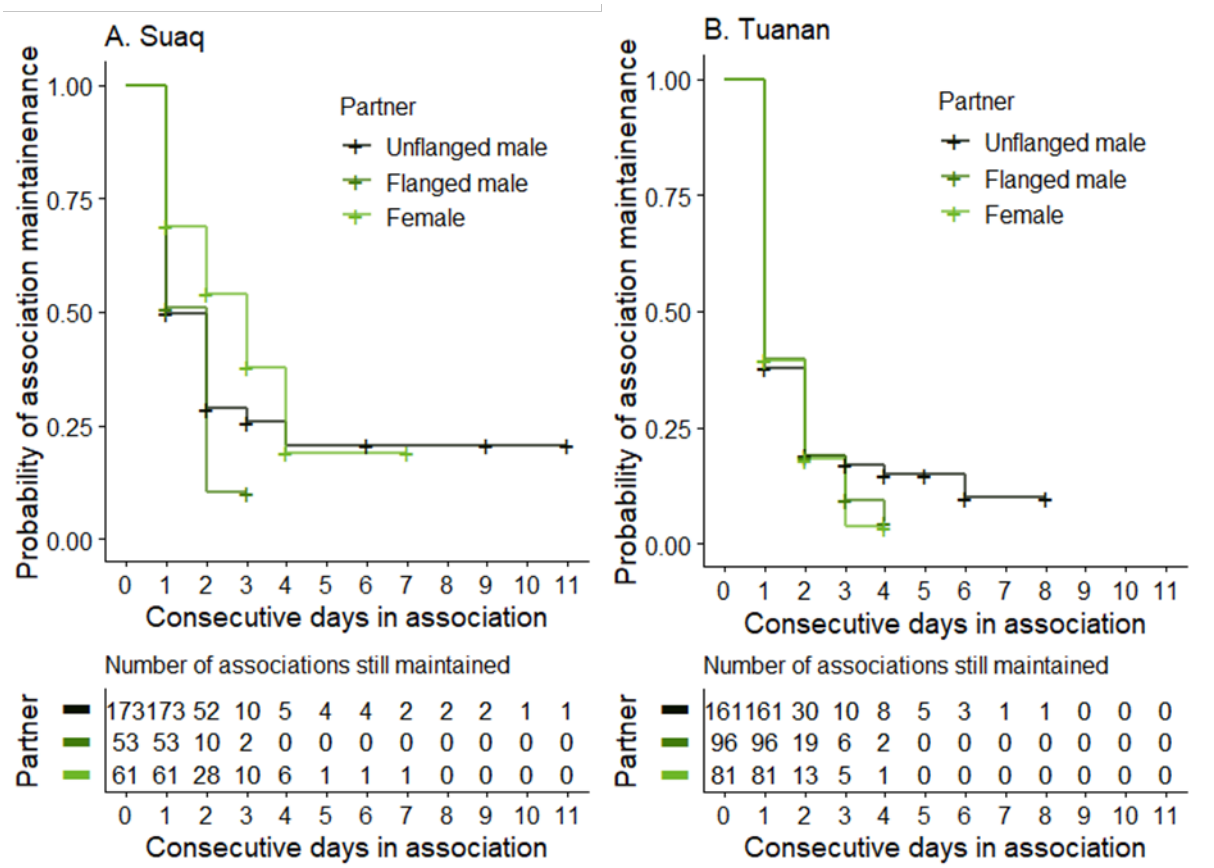

Figure 12 Kaplan-Meier survival curve for the maintenance of associations over consecutive days at Suaq (A.) and Tuanan (B.) by the association partner type (colour). The survival curve is based on the female focal data from follow periods also including the non-full-day focal follows (e.g. days when an individual was found) (N=625 [Suaq: 287; Tuanan: 338] associations of 21 females and 168 different FPs). The left-censored data is indicated in crosses.

FCM levels

Female FCM levels increased with the number of consecutive days in association with a male (β=0.136±0.047, t=2.871, P=0.004; Figure 13; Table 7), but not with females (β=-0.082±0.085, t=-0.960, P=0.34). None of the other social factors, including daily association time with either females or males and the occurrence of aggression, further improved the model fit. Accordingly, the control model containing all physiological and ecological factors was improved significantly when adding the number of consecutive days with males ($\chi^2_{12,13}$=7.30, P=0.007, ΔAIC=5.30). Although one particular female (Desy), who had male associations over a course of 9 days, appeared to be the main driver for this result, there still was a trend for consecutive days with males leading to elevated FCM levels when this female was excluded (β=0.106±0.056, P=0.06, N=333 of 89 follow periods; comparison to control model: $\chi^2_{12,13}$=3.48, P=0.06).

Because our data set only contained data for at most 4 consecutive days of female-female associations, we restricted the data set to sample days of at most 4 consecutive male-female association days in a further analysis. Then the effect of consecutive days in association with males on female FCM levels was no longer significant (β=0.082±0.062, P=0.19, N=361 of 96 follow periods). To evaluate if it was the total number of consecutive days spent with any association partner or only with males in particular which led to increased FCM levels, we tested if the increasing number of consecutive days in association with any partner led to increased FCM levels: The model was not improved ($\chi^2_{12,13}$=2.48, P=0.12, ΔAIC=0.48) nor was there a significant effect of consecutive association days (β=0.071±0.046, t=1.586, P=0.11) on FCM levels. In sum, it appears that only prolonged male-female associations over more than four consecutive days lead to increased female FCM levels.

Table 7 LMM output for female FCM level changes [z-ln(FCM concentration (ng/g))] in response to various ecological, physiological and social factors (comparison to control model [containing only ecological and physiological factors]: $\chi^2_{12,16}$=9.13, P=0.06, ΔAIC=1.13, N=370 of 89 FPs; comparison to null model: $\chi^2_{3,16}$=16.09, P=0.24, ΔAIC=9.91). All fixed effects with P<0.05 are indicated in bold. (z = fixed effect variable was z-transformed prior to analysis; C= control factor; F=fixed factor).

	Type	Estimate	SE	t value	P value
Intercept		*-0.193*	*0.390*		
Site (Suaq vs. Tuanan)	C	-0.018	0.281	-0.063	0.950
Consecutive days in association with female(s)	F	-0.082	0.085	-0.960	0.338
Consecutive days in association with male(s)	F	0.136	0.047	**2.871**	**0.004**
Male-female cumulative aggression index	F	-0.110	0.118	-0.933	0.352
Female-female agonistic interactions (no vs. yes)	F	0.063	0.443	0.141	0.888
Number of days followed	C	-0.002	0.018	-0.142	0.887
z Daily feeding proportion	C	-0.070	0.053	-1.325	0.186
z Age of dependent infant (y)	C	0.007	0.121	0.058	0.954
z Fruit Availability Index	C	0.053	0.072	0.735	0.464
Hour of sample collection	C	0.004	0.025	0.149	0.881
z Days to sample extraction	C	0.067	0.082	0.811	0.419
Laboratory (DPZ vs. IPB)	C	0.027	0.202	0.134	0.894
Total samples available with behavioural reference	C	0.005	0.008	0.560	0.577

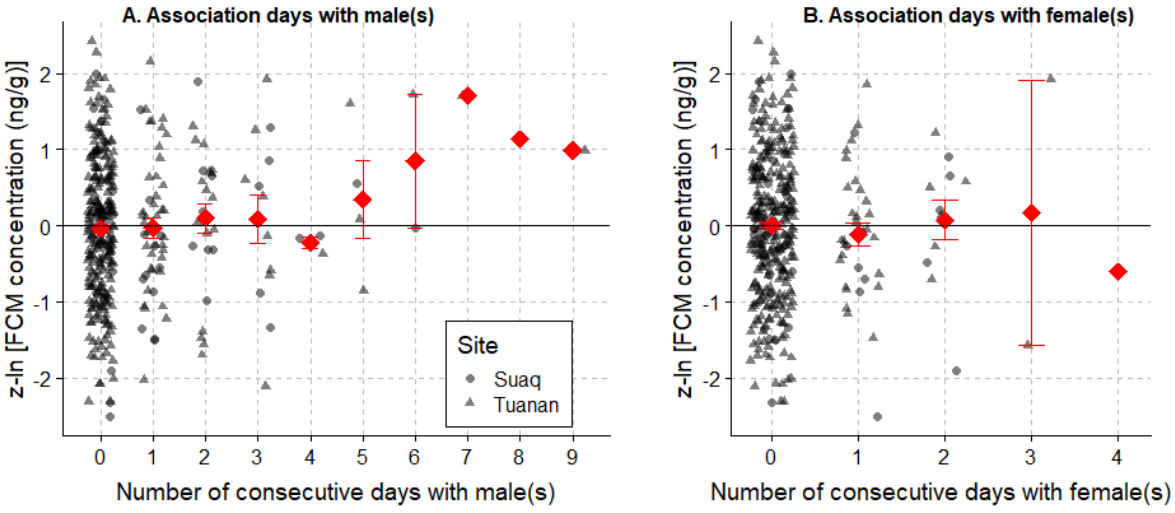

Figure 13 Standardized FCM levels (z-ln [FCM concentration (ng/g)]) (y-axis) of females in response to consecutive association days with adult males (A.) and to consecutive association days with adult females (B). A jitter function was added to the plot to visualize the overlapping data points (consecutive days are only integers). *Note:* The red diamond shaped points indicate the mean FCM levels with the error bar in red.

Discussion

Foraging cost of association

Because female reproductive success is generally directly linked to access to resources (Thompson et al. 2007; apes: Emery Thompson et al. 2008; Stumpf et al. 2008; orang-utans: Knott et al. 2009), the energetic costs of association with conspecifics have been held responsible for the varying degree of gregariousness across the orang-utan geographic distribution (van Schaik, 1999). The females in our study likely suffer energetically from associations (with both males and adult females): In both study populations, females increased the length of their active day, but their feeding time decreased both

absolutely (suppl. mat.) and relatively to moving time. This reduction is not only a trade-off directly resulting from increased time spent in social interactions, because 1) we controlled for time spent in social interactions, and 2) in the more sociable Sumatran population, feeding time was less affected by time spent in association with females. Hence, the reduced F:M ratio and the increased active time can be taken as direct evidence for elevated scramble competition, indicating that associations incur energetic cost to females. However, our measure of F:M ratio is very approximate and more accurate measures of actual energy intake and measures of energy balance, such as analysis of urinary C-peptide concentrations (e.g. Emery-Thompson and Knott, 2008), are needed to more directly assess the energetic costs of sociality in orang-utans. We can conclude that females modify their activity budgets, when in association with both males and females, in patterns that are congruent with increased scramble competition.

Orang-utan females likely do not gain direct benefits from associations with males, whereas males need associations with females to monitor their reproductive status. First, affiliative social interactions were extremely rare and genital investigations by males and male-initiated sexual interactions were the most frequent social interactions observed during male-female associations. However, benefits for females by associating with certain (flanged) males, such as protection from harassing males, cannot conclusively be ruled out (Fox, 2002; Mesnick, 1997). Second, most associations were both male-initiated and male-maintained, regardless of female reproductive state, i.e. the age of the female's dependent offspring, and females likely incurred costs from those involuntary associations as discussed above. When females are ready to conceive, however, they may actively seek the association with (dominant) flanged males (Fox, 1998, 2002; Spillmann et al., 2010). With our analyses, we did not capture this short window around conception. We conclude that females and males are likely at odds about association maintenance. Accordingly, orang-utan females have been reported to actively avoid male associates or try to end associations as rapidly as possible (Fox, 2002; Knott et al., 2018; Mitra Setia and van Schaik, 2007; Spillmann et al., 2010; Utami Atmoko et al., 2009a; van Noordwijk and van Schaik, 2009). Further investigations to understand how and if females attempt to avoid male associates have to be conducted, including the analysis of simultaneous ranging data. In sum, our study indicates that females incur costs from male-maintained associations, but no clear immediate benefits (albeit perhaps indirect ones: chapter 4), especially during periods of lactational infertility (~ 6.5 years [van Noordwijk et al., 2018]). Costs of involuntary associations may be detrimental, particularly in a less productive habitat (Wich et al., 2011), because orang-utan females' reproductive success highly depends on the availability of resources (Knott et al., 2009).

Stress and association

Female FCM levels increased as they spent more days in association with males, but not with females. This social factor was the best and only predictor for FCM level changes. Thus, repeated days of increased active time and reduced F:M ratio led to a physiological stress response. Interestingly, this was not the case when in association with other females. This finding suggests that females can easily avoid lengthy associations with other females before associations become too costly. Conversely, males appear to profit from associations with females and they maintain associations over a longer time period than a female would. The behavioural data available support this conclusion: Female-female associations never lasted more than 4 consecutive days at Tuanan, where the F:M ratio decreased significantly more when in association with other females than at Suaq, while male-female associations could last up to 8 days. The elevated FCM levels of captive orang-utan females when artificially confined to permanent association with males (Amrein et al., 2014) further support our hypothesis that increased sociality over an extended time period leads to a physiological stress response, especially in Bornean orang-utans. The findings in captivity suggest that Bornean females show stress reactions to extended sociality even in the absence of reduced net energy intake, suggesting that in captivity

increased FCM levels in females associated with males more likely reflect social rather than energetic stress. Although our endocrine data set is very limited, especially for the extended consecutive association days with males, we propose that only extended association periods with males lead to increased FCM levels as seen in captivity. However, whether these FCM elevations observed in our wild females are a response to the association itself or, alternatively, reflect energetic constrains due to the association-related decrease in feeding time and increase in activity patterns is unclear. Before this can be answered, future studies should generally aim at obtaining larger sample sizes for endocrine data linked to consecutive association days to obtain a more conclusive data set.

Following the same line of argument, one would expect to find more pronounced FCM level changes in the less sociable Bornean orang-utans in response to involuntary associations compared to Sumatran orang-utans. Although we could not find any evidence for differences in FCM level changes between Suaq and Tuanan, our data set was very small for the Suaq population (N=52 samples, a maximum of 6 [known] consecutive days in male-female association). Thus, the comparison should be repeated with a more extensive data set in the future. A difference in the physiological response to social stressors, including energy balance, may be expected in the light of the socioecological theory, because the degree of sociability between the two populations differs in the wild (van Schaik, 1999) and female-female associations were maintained over more consecutive days at Suaq than Tuanan, accordingly. Since our activity and feeding data indicate that both associations (with females) and social interactions are costlier to Tuanan females than to Suaq females, where fruit availability is generally higher (Wich et al., 2011), a stronger physiological stress response would be expected at Tuanan. Future studies are, however, needed to test this hypothesis and thus to evaluate whether females of the more sociable Sumatran orang-utan may be more "stress-resistant" which could explain why there is less need for either behavioural or physiological mechanisms to avoid associations.

We found no evidence for differences in female FCM levels on days with any agonistic interaction with either males or females in the two populations. Even though days with copulations were characterized by increased active time and reduced F:M ratio at Tuanan, we found no evidence that male aggression, in particular sexual coercion (suppl. mat. Sfigure 9), imposed any additional costs, either as reduced feeding time or in elevated FCM levels. If these forced copulations are cost insensitive, they would not qualify as sexual coercion by the definition of Smuts and Smuts (1993) (*"use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female"*), while the male-maintained associations would. However, the absence of a stress response does not exclude other costs of forced copulations, such as the limitation to the expression of female mating preferences. Indeed, the consistent attempts by females to escape from involuntary associations (Fox, 2002; Knott et al., 2018) suggest that females perceive resisted copulations as undesired rather than as a way to assess mate quality. For now, therefore, interpreting forced copulations as sexual coercion remains the most plausible explanation.

Since faecal cortisol metabolite levels represent an integrative measure of pooled endocrine activity over several hours or days (Hodges and Heistermann, 2003), it is likely unsuited to detect stress short-term stress responses to a specific behavioural event. Forced copulations lasted on average 8.8 ± 7.2 min (chapter 4), and a stress response associated with this behaviour is likely to be too short to be detected by our FCM measure. Urinary cortisol levels may thus be a more appropriate measure to assess whether particular social interactions induce more immediate elevations in cortisol production (e.g.: Silk et al., 2013) as has been shown for chimpanzees (Emery-Thompson et al., 2010; Muller et al., 2007). Further detailed studies, with a larger sample size and more immediate measures of cortisol levels from urine, are needed to examine whether female orang-utans do indeed not show stress responses to forced copulations.

The male perspective

Both unflanged and flanged males are responsible for maintaining associations, independent of the females' dependent offspring age (as a proxy for reproductive state), which supports the hypothesis that the males' interest to associate exceeds that of the females. Besides mating opportunities, these associations may be an attempt to monitor a female's reproductive state and sexual activities. In the absence of any apparent signal of fertility (Nunn, 1999), it remains uncertain how males detect female reproductive state, if at all. The genital investigations reported here may provide some olfactory information to males (review Drea, 2015; chimpanzee: Matsumoto-Oda et al., 2003), but data are insufficient to know how and if these relate to sexual interactions. It is likely that males also incur energetic costs from associations and interactions with females (Eastern chimpanzees: Emery-Thompson and Georgiev, 2014; Georgiev et al., 2014), and our unpublished data suggest this, too, for orang-utan males. Thus, males may have a set of decision rules when and for how long to associate with certain females. Accordingly, the time in association with males increases with the increasing age of the dependent offspring of females (this study; van Schaik 1999), suggesting some type of reproductive benefits for males. More detailed analyses on the social context of associations will provide further insight on how males benefit from sociality with females.

Conclusion

Here, we report evidence for sexual conflict over associations in orang-utans. We conclude that females incur costs from male-maintained associations, especially if those associations last multiple days. The costs include reduced feeding time, but increased moving and resting time, which adds up to longer activity periods. Furthermore, prolonged associations with males appear to be associated with elevated FCM levels, whereas this was not the case for female-female associations which were usually much shorter. We suggest that the absence of morphological fertility advertisement in female orang-utans may be explained by these costs of association, thus supporting the first prediction of the 'cost-of-sexual-attraction' hypothesis (Wrangham, 2002) for orang-utans. The length of sexual attractivity negatively correlates with the cost of association for females in the genus *Pan* (Wrangham, 2002). Orang-utans fit into this fission-fusion continuum at the solitary end: They do not exhibit any morphological signal of fertility, which would attract too many competing males at once leading to a prolonged period of unacceptably high energetic costs for the females, in addition to the mere physiological costs associated with the swelling itself (for a review: Nunn 1999). On the contrary, female orang-utans advertise non-availability with small labial swellings during pregnancy (Galdikas, 1981), likely to reduce the costs of association as males refrain from associating with pregnant females.

Yet, females of both *Pan spp*. and *Pongo spp*. exhibit unpredictable ovulation, albeit to varying extent (Deschner et al., 2004; Douglas et al., 2016; Nadler, 1981), which has been linked to paternity confusion serving infanticide avoidance strategies (Hrdy, 1979; Hrdy and Whitten, 1987; van Schaik et al., 2004). The concealed ovulation (Nadler, 1981) in orang-utans may therefore also serve to reduce the risk of infanticide as it does in most other primates (Hrdy, 1979; van Schaik et al., 2004). Female orang-utans seem to vary their mate preferences with their reproductive status accordingly (Knott et al., 2010). However, the evidence for infanticidal attacks by males remains weak (Beaudrot et al., 2009; Knott et al., 2019) and infant mortality is generally extremely low (van Noordwijk et al., 2018), suggesting that male infanticide in orang-utans is extremely rare compared to chimpanzees and that females employ efficient counterstrategies.

In a dispersed mating system with high association costs, and where males generally drive association patterns as found here for orang-utans, the lack of morphological fertility advertisement can be explained by the selection on the total concealment of ovulation. Given a risk of infanticide (Knott et al., 2019, 2010), females must achieve an optimum distribution of paternity assessments (van Schaik

et al., 2004; van Schaik and Janson, 2000) by removing as much information on female fertility status as possible. Accordingly, the absence of morphological fertility advertisement combined with the concealed ovulation in orang-utans appears to be the result of a trade-off between the costs of association and the necessity for paternity confusion (Knott et al., 2019, 2010; van Schaik et al., 2004). Future work will have to elaborate on the details of this hypothesis.

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Chapter 4: Making Sense of Female Orang-utan Extended Sexuality

Julia A. Kunz[1], Guilhem J. Duvot, Maria A. van Noordwijk[1], Erik P. Willems[1], Misdi bin Abdullah[2], Tony Weingrill[1], Carel P. van Schaik[1]

1) Department of Anthropology, University of Zurich, Switzerland
2) Faculty of Biology and Primates Research Center Universitas Nasional, Indonesia

Abstract

Orang-utan sexual behaviour is one of the most ambiguous among primates. Unlike some other promiscuous catarrhine primates, females do not advertise their fertility with a clear morphological signal, and both female-resisted and extremely proceptive copulations have been reported. Here we evaluate the occurrence and nature of orang-utan sexual interactions based on longitudinal behavioural data of several nulliparous and parous females with known or estimated timing of conception at two long-term study sites, Tuanan (*Pongo pygmaeus wurmbii*), Central Kalimantan, and Suaq (*Pongo abelii*), South Aceh, where data were collected over 15 and 10 years, respectively.

Female orang-utans were observed to mate multiple times with several males over a period of up to several years prior to conception. In fact, many sexual interactions occurred during periods when females were unlikely to conceive. Over 90% of sexual interactions were male-initiated, and the probability of copulation increased as the time of conception approached. Unflanged males were the immediate main driver of the extended female sexuality, as they exhibit higher copulation rates than flanged males. Accordingly, sexual conflict may be more pronounced between females and unflanged males, not only because the latter are less preferred, but because they initiate sexual interactions more frequently than flanged males, especially during periods when females are likely to be not fertile. While nulliparous females decreased rates of resistance to male-initiated sexual interactions with approaching time to conception, parous females' resistance rates remained constant, independent of the time to conception. Thus, besides male quality and time to conception, other factors appear to affect parous female resistance behaviour (chapter 5). From an ultimate perspective, female orang-utans may profit from not signalling fertility and concealed ovulation to distribute paternity probabilities among several males and thus reduce the risk of infanticide in a dispersed polygynandrous mating system.

Keywords: female mating strategies, infanticide avoidance, *Pongo ssp.,* sexual coercion

Introduction

In many primates, females may be sexually receptive despite not being fertile (Hrdy, 1979; van Schaik and Janson, 2000). Explanations for the occurrence of extended female sexuality, which leads to multiple and polyandrous mating, are varied across taxa (reviewed in Thornhill and Gangestad, 2008; van Noordwijk and van Schaik, 2000). Sexual attractivity, mating and consorting with males carries various costs (sexual swellings: Nunn, 1999, disease transmission: Nunn, 2003; energetic costs: Huchard et al., 2011; Muller et al., 2007; Stumpf and Boesch, 2005; Wrangham, 2002). Females should therefore gain some indirect or direct fitness benefits. First, they may gain genetic benefits by mating with multiple males through sperm competition mechanisms. Thus, good (Andersson, 1994) or compatible genes (Setchell and Huchard, 2010; Zeh and Zeh, 2001) may be favoured and thereby female preference may enhance the offspring's fitness. Second, females may reap male services either for themselves or for their offspring: Protection from conspecific males (Mesnick, 1997; Smuts and Smuts, 1993; van Schaik et al., 2004; van Schaik and Janson, 2000), access to resources (canids: Alea et al., 2017; chimpanzees: Deschner and Boesch, 2007; but see: Gilby et al., 2010), or direct infant care (Buchan et al., 2003; van Schaik and Paul, 1996).

The prolonged period of sexual activity in catarrhine primates is most parsimoniously explained as a female paternity confusion strategy to counteract the risk of infanticide (Hrdy, 1979; Hrdy and Whitten, 1987; van Schaik et al., 2004, 1999; van Schaik and Janson, 2000). Females exhibit not only extended periods of sexual activity around ovulation, but also often multiple cycles before conception, and continue to mate during pregnancy (Western chimpanzees: Deschner et al., 2004; bonobos: Douglas et al., 2016; Assamese macaques: Fürtbauer et al., 2011; review: van Schaik et al., 2000). The loosening of the link between mating and conception allows females to avoid complete monopolization by one dominant male, especially in non-seasonally breeding species living in multi-male groups (Drea, 2005; Hrdy and Whitten, 1987; van Schaik et al., 2004). A female's promiscuous mating strategy unwittingly skews male paternity assessments of several males in the females' favour, such that the risk of infanticide is minimised because males that have mated are likely to refrain from committing infanticide and may even defend the female's infant against attacks (e.g. Hanuman langurs: Borries et al., 1999; review and modelling approaches: Clarke et al., 2009; van Schaik et al., 2004). It is thought to reflect the outcome of an informational arms race between the males' ability to obtain information on the female reproductive state and the females' ovulation concealing strategies (see also Kokko, 2005; Stumpf et al., 2011). Accordingly, the observed mating pattern in a species reflects the balance between the gains to a female's fitness from efforts at achieving an optimal distribution of paternity probabilities and her fitness costs of coercion by males aiming at controlling female sexuality (Clarke et al., 2009; Emery-Thompson et al., 2008; Huchard et al., 2011; Muller and Wrangham, 2009; Smuts and Smuts, 1993; van Schaik et al., 2004).

Even though the females' costs from mating likely exceed those of males (Andersson, 1994; Bateman, 1948; Trivers, 1972), males still incur costs from mating effort (chimpanzees: Emery-Thompson and Georgiev, 2014; review: van Schaik et al., 1999) and thus are selective with whom to mate and when (chimpanzees: Emery-Thompson and Wrangham, 2008; orang-utans: O'Connell et al., 2019). Therefore, male mating effort focuses on the females most attractive to them. Female attractivity should reflect fertility, and is perceived in several ways by males. First, males prefer to mate with parous, experienced females (e.g. chimpanzees: Muller et al., 2006). Nulliparous females may undergo a long period of sub-fecundity, especially in species with a slow life history (primates: Anderson, 1986; chimpanzees: Muller et al., 2006; Proctor et al., 2011; mandrills: Setchell and Jean Wickings, 2006), and are more likely to lose their first offspring due to inexperience or infanticide (orang-utans: Knott et al., 2019; chimpanzees: Pusey, 2012; gorillas: Robbins et al., 2006). Second, females may exhibit physiological signals of fertility, such as olfactory cues (for a review: Drea, 2015; chimpanzees: Matsumoto-Oda et al., 2003; elephants: Bagley et al., 2006) or sexual swellings (gibbons: Barelli et al., 2008; chimpanzees: Deschner et al., 2004; Emery-Thompson and Whitten, 2003; baboons: Gesquiere et al., 2007; Higham et al., 2008), which function as (unreliable) graded signals of the probability of ovulation (Nunn, 1999; Zinner et al., 2004, 2002). Third, female proceptive behaviour may advertise

fertility to males often in combination with other (imprecise) signals (long-tailed macaques: Engelhardt et al., 2005; Eastern chimpanzees: Fallon et al., 2016; Hanuman langurs: Heistermann et al., 2001; capuchins: Janson, 1984; Sumatran orang-utans: Schürmann, 1981; Western chimpanzees: Stumpf and Boesch, 2006).

Because orang-utans have inter-birth intervals that are exceptionally long and variable (7.6 ± 2 y), even compared to other great apes (van Noordwijk et al., 2018), males would profit from having accurate information on female reproductive state. However, orang-utan females do not exhibit any apparent morphological signals of fertility (Galdikas, 1981; Schultz, 1938) and it remains unclear if and how orang-utan males can assess the fertility status of females. Although males frequently investigate the genitals of females and may gain some olfactory information (Schürmann, 1981), both in captivity (Nadler, 1981) and the wild (Fox, 1998; Knott et al., 2010), males have been reported to copulate with females regardless of their ovulatory state. Further, it has been argued that the size of the infant of parous females and her proceptive behaviour may provide (crude) information on her reproductive state (Fox, 1998).

The reproductive physiology of wild orang-utan females is still poorly understood (Knott et al., 2009). Although reproductive hormone levels and conception are generally linked to food availability, and conception is unlikely when fruit is scarce (Knott et al., 2009; MvN, unpubl. data), it remains unknown, if and how many non-conceptive cycles females experience before conception (Stumpf et al., 2008). Wrangham's (2002) 'cost-of-sexual-attraction' hypothesis suggests that the absence of fertility advertisement in orang-utans may be the result of a trade-off between ecological constraints on associations and the need for paternity confusion (chapter 3). Thus, female orang-utan sexuality seems to have been driven to some extent by an infanticide avoidance strategy (Knott et al., 2019, 2010). Female preference for certain males was reported to change with her reproductive state accordingly (Knott et al., 2010). However, this interpretation remains debated because there is limited evidence for sexually selected male infanticide in wild orang-utans (Beaudrot et al., 2009; but see: Knott et al., 2019; Scott et al., 2019), and infant mortality is generally extremely low (van Noordwijk et al., 2018; Wich et al., 2009), suggesting that infanticide, if it occurs, is generally rare. Nevertheless, orang-utans meet the primary biological criterion for vulnerability to infanticide, namely a lactation to gestation ratio exceeding one by far (van Schaik, 2000). In addition, there are various other species in which infanticide is quite rare, and female sexuality nonetheless fits all the predictions of an anti-infanticide strategy (Hrdy and Whitten, 1987), suggesting that females employ efficient counterstrategies (Lukas and Huchard, 2014; Palombit, 2015).

Reported patterns of sexuality in wild orang-utans remain inconclusive, as mating is relatively rare, especially on Borneo (e.g. Knott et al. [2010]: 21 copulations in 45 500 h at Gunung Palung, West Kalimantan; Morrough-Bernard [2009]: 15 copulations in 2 years at Sabangau, Central Kalimantan; Fox [1998]: 204 copulations in >9000 h at Suaq [on Sumatra]), because of their exceptionally slow life history (van Noordwijk et al., 2018; Wich et al., 2009) and semi-solitary lifestyle (MacKinnon, 1974; Rijksen, 1978; van Schaik, 1999). Female orang-utans express strong mate preferences, both positive and negative (Fox, 1998, 2002; Knott et al., 2010). On the one hand, there are rare observations of extremely proceptive sexual interactions, where females masturbate males over extended periods prior to intromission (O'Connell et al., 2019; Schürmann, 1981; CvS unpubl. data). On the other hand, female resistance during sexual interactions is frequently reported, resulting in forced copulations (Galdikas, 1985b; Knott, 2009; Knott and Kahlenberg, 2007; MacKinnon, 1974; Rijksen, 1978; Utami Atmoko et al., 2009a).

The reported variability in orang-utan mating behaviour, especially the relative frequency of forced to unforced mating, across study sites and species may reflect small sample sizes, but has largely been attributed to female reproductive state (Knott et al., 2010; Nadler, 1981) combined with the variation in male quality and morph (Galdikas, 1985a; Knott, 2009; Schürmann, 1981; Utami Atmoko et al., 2009a; Utami Atmoko and van Hooff, 2004). Orang-utans exhibit a pronounced male bimaturism, which is associated with alternative reproductive strategies (Utami Atmoko and van Hooff, 2004).

Unflanged males lack secondary sexual characteristics (SSCs), may remain developmentally arrested up to more than 10 years (Dunkel et al., 2013; Utami Atmoko and van Hooff, 2004), are mostly subordinate to flanged males (Utami Atmoko et al., 2009b) and generally exhibit higher association, copulation and coercion rates than flanged males (Galdikas, 1985b; MacKinnon, 1974; Sugardjito et al., 1987; Utami Atmoko and van Hooff, 2004). There is evidence that the developmental arrest of SSCs is more pronounced in Sumatran (*Pongo abelii*) than Bornean (*Pongo pygmaeus*) orang-utans (Delgado and van Schaik, 2000; Dunkel et al., 2013). While in (West) Sumatran populations, one locally dominant flanged male is present over several years (Mitra Setia and van Schaik, 2007; Utami Atmoko and Setia, 1995; Utami Atmoko et al., 2009b), in Bornean populations dominance relationships among flanged males reportedly fluctuate strongly (Dunkel et al., 2013) and with it likely individual flanged males' condition (Knott et al., 2010; Spillmann, 2017).

In this study, we evaluate longitudinal data on the mating behaviour of female orang-utans from two long-term study sites, Suaq (*P. abelii*) and Tuanan (*P. pygmaeus wurmbii*), to assess if female sexuality is driven by paternity confusion strategies. First, we evaluate how mating frequency varies depending on study site, female parity and time to conception, the interaction partner, and ecological factors. Assuming that males do not have accurate cues of female fertility, we predict that mating behaviour is not only concentrated around the period of (known) conception, but occurs during an extended time window and with multiple males. Therefore, we also evaluate the number of mating partners and observed copulations per conception. Because males likely also experience costs from both associating and mating with females (unpubl. data), we expect that males exhibit a preference for 1) parous over nulliparous females and 2) for parous females who are closer to conception. Second, we evaluate female resistance to male mating initiations, as it may settle on periods when females are not fertile and hence, rather reflect female reproductive state than female negative choice against specific males or male morphs due to male quality. Further, we assess the initiation and duration of the sexual interactions in more detail depending on female behaviour.

Methods

Study site and study subjects

We evaluated long-term, behavioural data of two study sites: Tuanan, Mawas Reserve, Central Kalimantan, Indonesia (02°15'S; 114°44'E) and Suaq, Gunung Leuser Nationalpark, South Aceh, Indonesia (03°02'N; 97°25'E). All the data were collected by well-trained observers according to the established behavioural data protocol (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). At Tuanan data was collected between July 2003 and July 2018. At Suaq, data was collected between June 2007 and March 2018. At Tuanan, male dominance relationships are generally unstable and confrontational assessment is common among flanged males (scars from physical fights: Dunkel et al., 2013; long call response rate: Spillmann et al., 2017). At Suaq, Islo was the locally dominant male from the onset of the study period (June 2007) until he was found wounded in early 2014. Since then, Islo was still occasionally seen in the study area, long calling and being sexually active until March 2018, but females did not actively approach his long calls (pers. obs.). However, since 2014 no other male seemed to consistently attract females and displace all other males either. Thus, the period from January 2014 to March 2018 was likely a period with unstable male dominance relationships at Suaq.

Because of the long-term data collection effort, the subjects were individually recognized and longitudinal data on both females and males available. We determined individual identity through both visual inspection of photographs and genetic data (Arora et al., 2012; van Noordwijk et al., 2012). The reproductive state of females was derived from the birth of their dependent offspring. We calculated the timing of conception by back-dating 245 days from the estimated or known date of birth (C Graham, 1988). In this study, we only included females for whom the date of conception could be estimated from the known subsequent birth (Table 8; cf. van Noordwijk et al., 2018). This reduced our data set considerably, yet it allowed us to more accurately assess how sexuality changes with an individual

female's approaching conception. We distinguished between nulliparous, adolescent females who conceived their first infant, and parous females, who were in continued association with their dependent offspring. We regularly used non-invasive quick urine tests at both study sites to assess pregnancy directly in the field using (cf. Knott et al. 2010). From these tests, we know of one failed pregnancy at Tuanan (MvN, unpubl.). Thus, although failed pregnancies occurred, they are unlikely to have affected the broader patterns because they appear to be rare.

Table 8 Overview of the data available for each individual female and conception (indicated by the infant name which was conceived)

				Focal follow data		*All-occurrence data on sexual interactions*			
Site	**Female ID**	**Parity**	**Conceived infant**	**Follow hours[$]**	**Nr of FP[§]**	**First cop** [relative to conception (y)]	**Last cop** [relative to conception (y)]	**Total cops *(excl. attempts)***	**Total resisted cops**
Suaq	Chindy	nullip.	Chips [6m]	74	0	-4	-4	1	0
Suaq	Ellie	nullip.	Eden [1m]	517	1	-0.2	-0.1	4	0
Suaq	Lilly	nullip.	Luther [1y]	301	0	-1.4	-1.3	3	1
Suaq	Tina	nullip.	Taylor [1y]	348	0	NA	NA	0	0
Suaq	Cissy	parous	Cinnamon [1m]	204	0	-3.4	-0.4	8	5
Suaq	Dodi	parous	Dalia [1m]	61	0	-1.7	-1.4	5	1
Suaq	Friska	parous	Frankie [1y]	671	2	-4.1	-0.7	4	2
Suaq	Lisa	parous	Leon [1m]	1282	10	-4.7	-0.1	68	58
Suaq	Lisa	parous	Lois [6m]	313	1	-2.3	-1.8	14	10
Suaq	Raffi	parous	Redang [1y]	167	0	NA	NA	0	0
Tuanan	Juni	nullip.	Jip [known]	1302	6	-1.4	0	30	6
Tuanan	Kondor	nullip.	Kahiyu [1m]	1461	9	-2.3	-0.4	31	11
Tuanan	Milo	nullip.	Merkur [1m]	1734	14	-3.1	0.2	24	0
Tuanan	Cinta	parous	Caka [6m]	162	0	-0.2	0.2	5	3
Tuanan	Desy	parous	Danum [6m]	857	4	-4.2	-0.4	12	10
Tuanan	Desy	parous	Darwin [known]	914	8	-1.9	0.2	7	3
Tuanan	Inul	parous	Ipsy [6m]	63	0	-0.5	-0.5	1	0
Tuanan	Inul	parous	Iyan [1m]	267	0	-4.7	-0.5	2	2
Tuanan	Jinak	parous	Joya [6m]	4169	33	-4.3	0.3	5	2
Tuanan	Juni[£]	parous	Jane [1m]	2977	19	-1.7	0.1	13	2
Tuanan	Juni	parous	Jena [1m]	1677	13	-3	-0.1	8	5
Tuanan	Kerry	parous	Ketambe [known]	2807	21	-3.2	0.2	23	3
Tuanan	Kerry	parous	Kino [1m]	1438	10	-2.6	0.1	32	2
Tuanan	Kondor[+]	parous	Kecap [6m]	172	2	0	0	1	1
Tuanan	Kondor[+]	parous	Kilmino [6m]	280	8	0.1	0.1	3	0
Tuanan	Mindy	parous	Mawas [1m]	3068	21	-1.9	0	3	3
Tuanan	Mindy	parous	Moby [1m]	2312	20	-1.4	-0.2	3	1
Tuanan	Pinky	parous	Pina [known]	446	4	-3.1	0	8	4
Tuanan	Sidony	parous	Sony [known]	162	1	NA	NA	0	0
Tuanan	Tina	parous	Tuktuk [6m]	19	0	-0.3	-0.3	1	1

Footnotes:

Females may appear repeatedly in the table with different infants, because they conceived more than once during the study period. All the information on one row is relative to the conception of the infant indicated. Some females may appear in this table, but were not included in all the analyses when too few follow hours (<200) were available.

The estimated or known birth of infants which were conceived are indicated as follows*: known* = exact birth date of infant is known; *1m* = infant was seen within the first month after the birth; *6m*= infant was seen within the first 6 months after birth; *1y* = infant was seen within the first year of birth.

[$]**=** Total of focal follow hours available for a conception of a particular female up to the birth of her infant. This includes all focal follow data, not only full-day focal follows.

[§] **=** Number of follow periods included in the analysis on the occurrence of male-initiated copulations

continued on p. 80

continued from p. 79
[+]= Kondor lost her first two infants [Kahiyu and Kilmino], so the conception period of Kilmino and Kecap were extremely short and had to be excluded from the main analyses.
[£]= Juni experienced a known, failed pregnancy during this conception cycle [i.e. positive pregnancy test]. She was still included in the analyses, because we cannot exclude that other females also experience [unknown] failed pregnancies.

Behavioural data

Focal animal behavioural data included recording the presence of association partners at 2 min intervals. All the individuals within 50 metres of the focal animal qualified as association partners. The daily time spent in association with either unflanged or flanged males was defined as the female's focal follow time when males where within 50m. Furthermore, we recorded sexual interactions and the identity of the interaction partner ad libitum (Altmann, 1974). We subdivided sexual interactions into 5 categories following the definitions of Fox (1998) (Table 9). All the definitions are directly based on the behaviour of the female. In this study, we refer to copulations, when intromission was achieved. All mating attempts when intromission was not achieved are labelled as attempts. Further, we regard copulations in which females were either passive or proceptive as *non-resisted* copulations in the analyses, and forced and passive copulations as *male-initiated* copulations. Because mating interactions often take place high up in the canopy and visibility may be obstructed by foliage, both the intromission duration and the presence/absence of ejaculation could not be assessed reliably for all copulations. The duration of sexual interactions was therefore defined as the duration of body contact between the interaction partners, and not the time of intromission *per se*.

Table 9 Definitions of sexual interactions used for this study adapted from Fox (1998).

Sexual interaction	Intro-mission	Initiator	Definition
Resisted copulation	*Yes*	*Male*	A male-initiated mating with achieved intromission despite the females' resistance. Female resistance may manifest itself by (repeated) attempt(s) to move away from the male, obstructing the male's attempt to position the female for intromission, slapping and biting the male to evade intromission, and is often, but not necessarily, accompanied by the female's squeal or scream vocalizations. Males may restrict females from moving away, often slap and bite the female. Importantly, females may not resist throughout the entire copulation, but only in the beginning/middle/end (Knott et al., 2010). Here, all the signs of female resistance at any time during a sexual interaction were lumped into a single category.
Non-resisted copulation	*Yes*	*Male*	Male-initiated copulation with achieved intromission. The female is passively allowing the male to copulate, but the female does not actively facilitate intromission (often she keeps on feeding).
Proceptive copulation	*Yes*	*Female*	Female-initiated and -facilitated copulation, with intromission achieved. Females actively approach the male, may present their genitals, investigate and handle the male's genitals and position themselves to facilitate intromission.
Resisted attempt	*No*	*Male*	Male attempts to copulate, but female resistance is successful and no intromission is achieved.
Proceptive attempt	*No*	*Female*	Female attempts to copulate with a male, but the male does not react to the female's proceptive advances (as described above in proceptive copulations) but no intromission is achieved.

We analysed two different behavioural data sets. The first data set ("*female focal follow data*") consisted exclusively of female focal follow periods (FP) of at least 5 full-day follows within 12 ± 8 (mean ± SD) days (median=9, [5, 77] days [min, max]) (N=1611 days of 13 different females, Table 8). The second *all-occurrence* data set on sexual interactions comprised data from both adult female (>50'000 h) and male (>29'000 h) focal follows. We combined female and male focal follow data, because both male-female associations (N=2107 [Suaq: 618; Tuanan: 1489]) and especially copulations were rare (N=482 [Suaq: 164; Tuanan: 318], i.e. <0.006 copulations per observation hour). Therefore, all observed sexual interactions of a female were included, either when she was the focal individual or the interaction partner during a male focal follow (i.e. association partner) (Table 8). When the all-occurrence data set was used in the analyses, we controlled for the time a female was observed (sum of focal follow hours and the time when in association with a focal male). We added the time in association

with males as a fixed effect in the models to avoid a bias towards females who were more frequently observed in association with males.

Ecological data

Female reproductive hormone levels reportedly rise with higher fruit availability (Knott et al., 2009) and conceptions are less likely when fruit availability is low (MvN, unpubl. data). At both study sites, fruit availability surveys were conducted on a monthly basis throughout the entire study period (Vogel et al., 2009), including ~1500 trees in Tuanan and ~1000 in Suaq. The Fruit Availability Index (FAI) reported here represents the percentage of trees with fruits over all surveyed trees (Harrison et al., 2010). Because at Suaq the FAI is generally higher than at Tuanan (Wich et al., 2011), the FAI was z-transformed within study site to have comparable values across the two sites (indicated by "zFAI") and to assess FAI effects within the study site.

Statistical analyses

All statistical analyses were conducted in R (version 3.5.2) using the packages 'lme4' (Bates et al., 2015) and 'lmerTest' (Kuznetsova et al., 2017). We set up (generalized) linear mixed models ([G]LMMs). For all models, we tested for multi-collinearity issues (VIF < 2), outliers and influential cases (Fox and Weisberg, 2018), and inspected the residual graphs visually to check for homoscedasticity. Further, models which assumed a Gaussian error distribution were checked for normality of the residuals. Here, we report the full models and the comparison to the control model, which included the random intercepts, the offset term and all control variables (if indicated as such). Models were compared using likelihood ratio tests. Furthermore, the pseudo-R^2 (delta-value for GLMMs) as obtained from the 'MuMIn' package (Barton, 2018) is reported. For binomial GLMMs the odd's ratio (OR) is indicated for all fixed factors. The P value of 0.05 was used as a cut-off value for significance. All figures were generated using the packages 'ggplot2' (Wickham, 2016) and 'cowplot' (Wilke, 2019). Whenever we report average values in the results, these are mean values with standard errors (SE).

Longitudinal analyses based on individual females

To assess the number of copulations and mating partners a female had per known conception (N=21 of 13 females), we formulated GLMMs with a Poisson error distribution using the *all-occurrence* data set. We only included females and conceptions for which at least 200 focal follow hours (including pregnancy) were available. We added the observation hours (mean=1384±SE 244 h) as an offset term to correct for sampling effort. All observed copulations (excluding failed attempts), both with and without female resistance, were included (see suppl. mat. for the results including only non-resisted copulations). The copulation frequency and the number of mating partners were quite variable between females (Figure 14) and adding female identity as a fixed effect to the Poisson GLM significantly improved the model fit (mating partner number: $\chi^2_{6,14}$=80.86, P<0.0001; Number of copulations: $\chi^2_{6,14}$=296.33, P<0.0001). To account for this variability, we included female identity as a random intercept. We added study site, female parity and the time spent in association with males as fixed effects. We tested for possible interactions between female parity and either association time and study site. Moreover, in the model for the number of observed copulations, we additionally included the number of mating partners as a fixed effect.

To evaluate when copulations occurred in relation to conception, we formulated a binomial GLMM to evaluate the occurrence of male-initiated sexual interactions on individual female full-day focal follows (N=1611 of 13 different females and 21 conceptions, Table 8) depending on study site, female parity, time to conception (y), time in association with either unflanged or flanged males, and fruit availability. The time to conception was a (negative) value in years and conception was set at time 0, positive values indicate that the female was pregnant. We tested if the time to conception related in a quadratic function to the observed copulation probability, with a peak around conception. Further, we took the cumulative daily hours spent with unflanged and flanged males, to account for multiple males

in association on certain days. Therefore, the hours spent with males may exceed the daily active time of a female, when multiple males were present. We z-transformed all continuous fixed factors to facilitate model convergence. Further, we tested for possible interactions between study site and all other fixed effects. The follow periods (FP) (N=209) nested in the female identity (N=13) were included as random intercepts to avoid pseudo-replication. Moreover, the daily active time was set as an offset term using a logit-link function to account for varying sampling effort (i.e. observation hours).

Cross-sectional data analyses on details of sexual interactions

First, we set up a binomial GLMM to evaluate when female resistance (0/1) occurred to male-initiated sexual interactions (*all-occurrence* data set) (N=304 sexual interactions). Study site, female parity, time to conception, male morph, the duration of the dyadic association, the total number of copulations during the dyadic association and local zFAI were included as fixed effects. We tested for various 2nd order interaction terms between either study site or female parity and any other fixed effect to evaluate if mechanisms may differ depending on site or female parity. Female identity was added as a random intercept (18 different females, also including females with less than 200 observation hours). Due to the (relatively) small sample size and the large number of different males (N=62), we could not account for male identity as a random intercept in the full model. In any case, adding male identity as a random intercept in the null model did not improve the model fit ($\chi^2_{2,3}$=0.236, P=0.63). Second, with the subset of all female-resisted sexual interactions (N=141 female-resisted sexual interactions of 15 different females), we set up a binomial GLMM to analyse when female resistance was successful, i.e. when intromission was not achieved. We included male morph, time to conception, female parity and the interruption by other males as fixed effects. We could not incorporate site differences in our analyses, because our data set was limited and we did not observe any resisted sexual interaction of nulliparous females from Suaq (suppl. mat. Stable 24). Again, only female identity, but not male identity, was included as a random intercept in the binomial GLMM. Third, we assessed if body contact duration differed between the sexual interaction types (female-resisted, non-resisted and proceptive copulations, and female-resisted and proceptive failed attempts) (N=485, increased sample size because time to conception was not included in this analysis). We set contrasts to first compare the copulations to attempts and subsequently the copulation types. We additionally built study site, female parity and male morph as fixed effects into the full model. Moreover, we included female (N=36) and male identity (N=88) as crossed random intercepts. For the subset of the copulations, for which more detailed behavioural data were available (N=170), we evaluated the occurrence of intromission breaks. Intromission breaks are defined as breaks of intromission during sexual interactions, often to reposition or due to female resistance and attempts of moving away from the male. The total duration of the sexual interaction was set as a fixed factor to account for the increased chance of intromission breaks the longer copulations lasted. We could only add female identity as a random intercept, because adding male identity would have made the model too complex (60 different male identities).

Results

Longitudinal data in relation to time to conception

Sexual interaction frequency and number of mating partners per conception

Sexual interactions were male-initiated in 90.7 % (335 of 369 interactions) of all interactions with known initiation. Conversely, female-initiated body contact was observed in only 7.8 % of all sexual interactions (29 of 369; the remaining 5 interactions were initiated by both male and female) (suppl. mat. Stable 25). There were not enough observations to assess female-initiated sexual interactions quantitatively in respect to time to conception, but we discuss them qualitatively in a separate section below. At both study sites, sexual interactions were observed well before the time of known conception in both nulliparous (Suaq: -1.9±SE 1.1 years before conception [N=3]; Tuanan:-1.7 ±SE 0.7 years [N=4]) and parous females (Suaq: - 3.3±SE 0.6 years [N=5 conceptions of 4 females];

Tuanan: -2.8±SE 0.5 years [N=15 conceptions of 8 females]) (Figure 14). Pregnancy copulations were observed up to the fourth month of gestation (N=34) (Figure 14). Figure 14 illustrates the variability between individual female mating frequency.

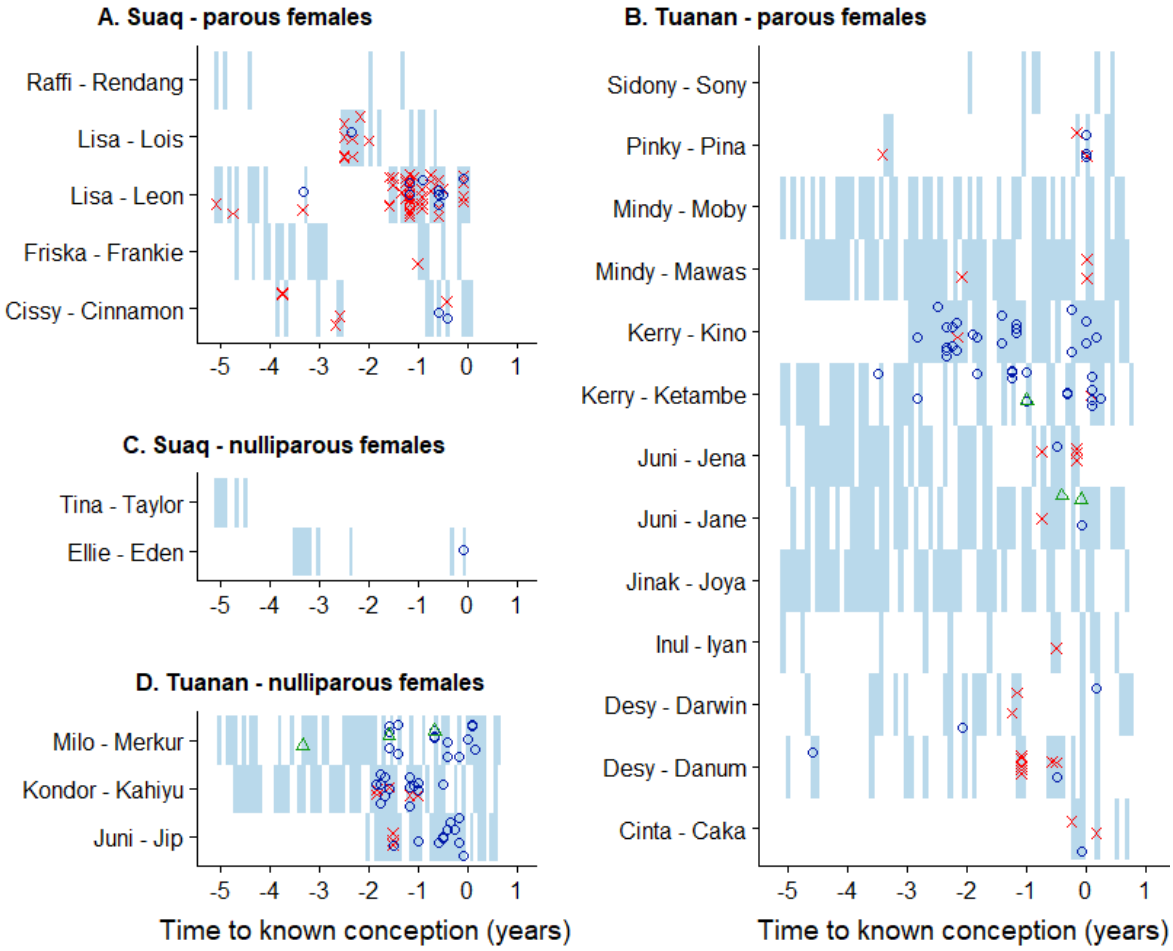

Figure 14 Observed copulations by the time to conception (y) by individual female conceptions (y-axis shows the mother and the infant conceived) divided by female parity (parous: A, B; nulliparous: C, D) and study site (Tuanan: B, D; Suaq: A, C). The blue shaded area represents all the periods when a female was the focal animal. Only females for which at least 100 focal follow hours for the conception were available are included. The red crosses show when a resisted copulation was observed, the blue circles when a non-resisted copulation occurred, and the green triangles stand for female proceptive copulations.

Females were observed to copulate on average 14.2 ±SE 3.5 times [minimum 0, maximum 68 copulations] with 4.6 ±SE 0.9 different males [minimum 0, maximum 16] per conception (N=21 conceptions; Figure 15; suppl. mat. Stable 26). As can be expected, the proportion of observation time spent in association with males was the best predictor for both the number of mating partners per conception (β=3.247±0.742, z=4.375, P<0.001) and the number of copulations observed (β=3.565±0.562, z=6.344, P<0.0001). The number of observed mating partners did not significantly vary between study site or female parity, but the number of observed copulations did (suppl. mat. Stable 26). At Suaq, nulliparous females exhibited lower copulation rates than parous females, whereas nulliparous females at Tuanan had higher copulation rates than parous females. The interaction between female parity and study site improved the model fit ($\chi^2_{6,7}$=12.99, P=0.0003), even when excluding Lisa (parous female at Suaq) who can be considered as an outlier with both a high number of mating partners (Figure 15) and a high mating frequency (Figure 14). The full models tested were significantly better than the null models both for the number of mating partners ($\chi^2_{2,5}$=14.84, P=0.002) and the number of copulations ($\chi^2_{2,7}$=66.9, P<0.0001).

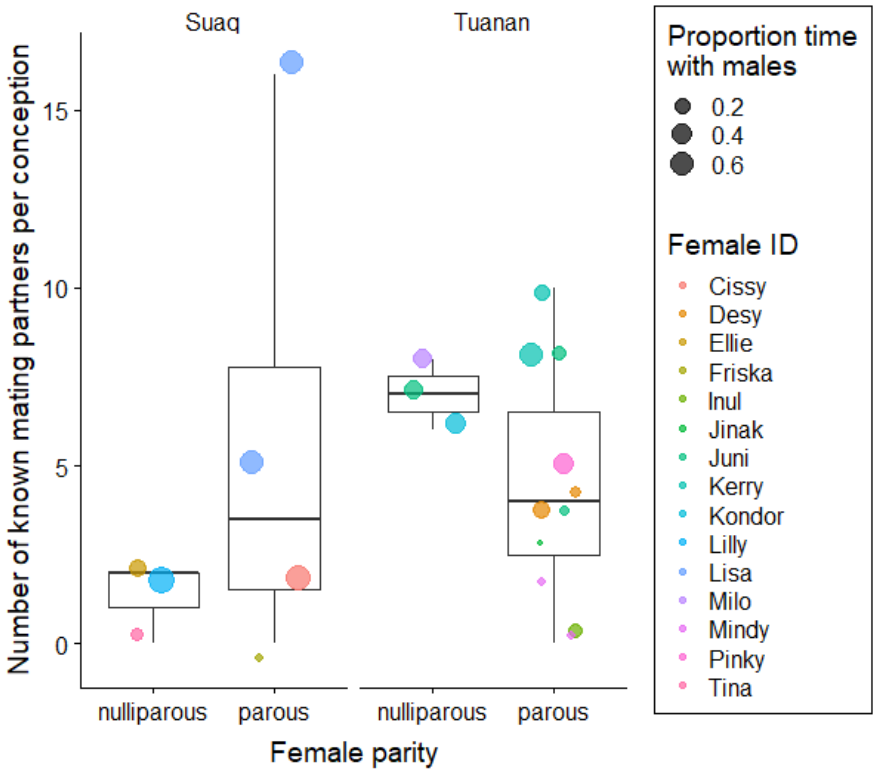

Figure 15 Number of mating partners per female and conception by study site and female parity. Different individuals are indicated in different colours, the size of the data points is relative to the proportion of time a female spent in association with males (for each of these conception rounds) (relative to the total time she was observed). Only females and their conception round for which at least 200 focal follow hours were available were included (Table 8). The boxplots are based on the median value (black bar), the box indicates the first and third quartile and the vertical lines reach to the minimum and maximum distribution.

When do males copulate?

When looking at the female focal follow data, the daily probability of male-initiated copulations increased as conception approached (β=1.225±0.323, OR=3.04, z=3.798, P<0.001) (Table 10; Figure 16). Male-initiated copulation probability did not differ between parous and nulliparous females (β= 0.193±0.549, OR=1.21, z= 0.351, ns.). Only the time spent with unflanged males predicted the occurrence of male-initiated copulations (β=0.996±0.114, OR=2.71, z= 8.697, P<0.001), but not the time spent with flanged males (β= -0.080±0.118, OR=0.92, z= -0.675, ns.). Although visual inspection of the data (Figure 16) suggested a difference of copulation rates between the sites, male-initiated copulation probability on a given female focal follow day did not differ significantly between Tuanan and Suaq (β= -1.159±0.731, OR=0.31, z= -1.586, ns.). Within sites there was no effect of zFAI on male-initiated copulations (β= 0.220±0.175, OR=1.25, z= 1.256, ns.). The full model was significantly better than the null model ($\chi^2_{3,9}$=113.75, P<0.0001; N=1611 full-day focal follow days of 13 different females (21 conceptions) and 209 FP).

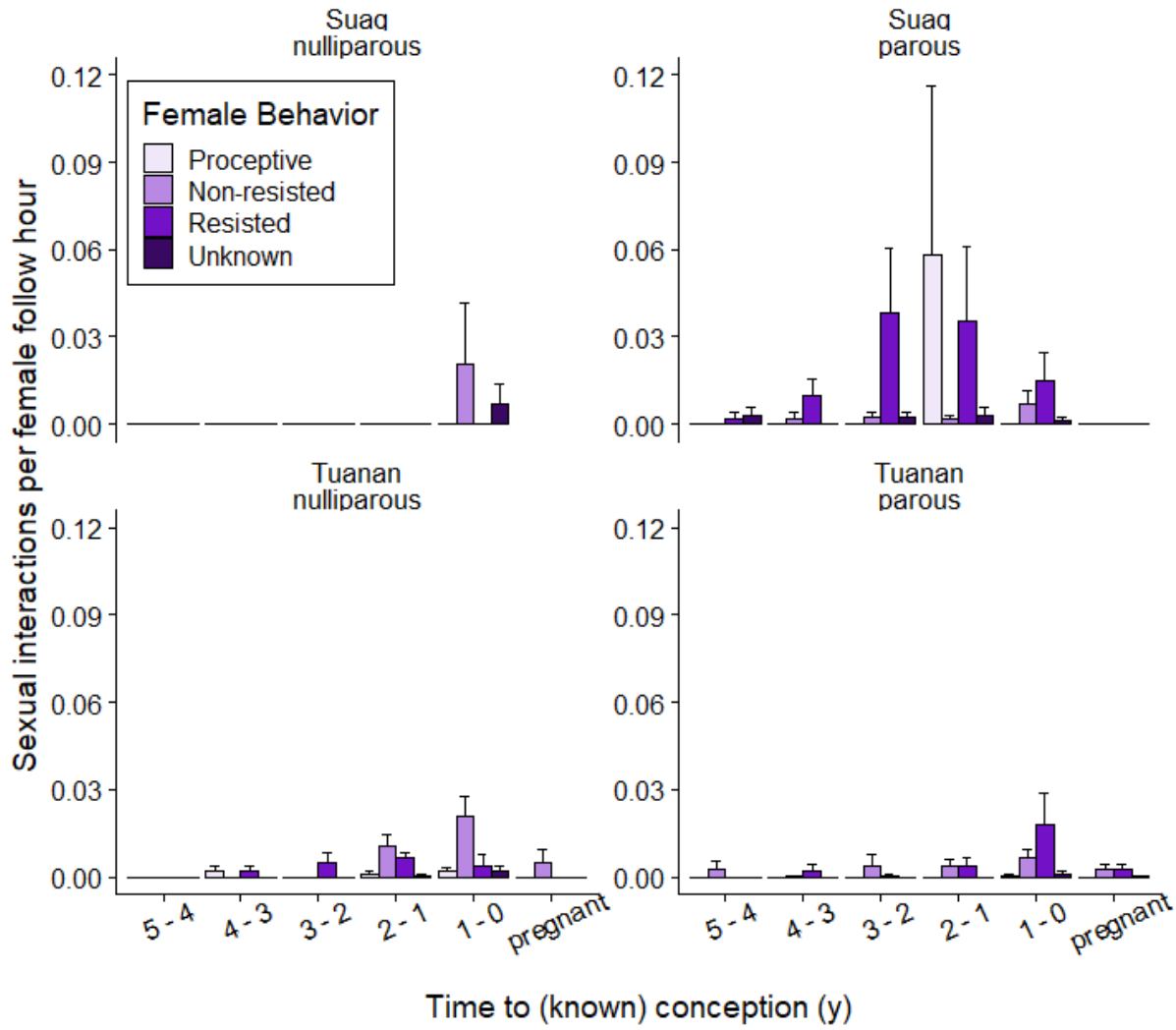

Figure 16 Increase of sexual interactions as conception approaches: Bar plot of all observed sexual interactions during female focal follows corrected by the total follow hours available per female and year to conception, depending on the females' behaviour (legend) by the study site (top: Suaq; bottom: Tuanan) and female parity (left: nulliparous; right: parous). The error bars are based on the standard error. Note: The x-axis shows the years to conception. The date of conception was inferred from the birth date of the offspring as indicated in Table 8. (Note: This figure also includes failed mating attempts and all the available female focal follow data is lumped; the absence of pregnancy mating at Suaq may be an artefact of the low observation time on pregnant females (Figure 14); also see Fox [1998]).

Table 10 Occurrence of male-initiated copulations: binomial GLMM output for the occurrence of male-initiated copulations on the basis of full-day female focal follows (N=1611 of 13 different females and 209 follow periods [≥ 5 full days per period]) by study site, female parity, time to conception, association time with flanged and unflanged males and Fruit Availability Index ($\chi^2_{3,9}$=113.62, P<0.0001, pseudo-R^2=0.21 [delta]). (Note: z= the values were z-transformed prior to analyses in order to facilitate model convergence).

Fixed effects	**Estimate**	**SE**	**Odd's ratio**	**z value**	**P value**
Intercept	-1.605	0.795			
Active time duration (h)	*Offset term*				
Site (Suaq vs. Tuanan)	-1.159	0.731	0.31	-1.586	0.113
Time to conception (y)	1.225	0.323	3.04	**3.798**	**<0.001**
Parity (nulliparous vs. parous)	0.193	0.549	1.21	0.351	0.725
z Association time with flanged males	-0.080	0.118	0.92	-0.675	0.500
z Association time with unflanged males	0.996	0.114	2.71	**8.697**	**<0.001**
z Fruit Availability Index	0.220	0.175	1.25	1.256	0.209

Cross-sectional detailed data on sexual interactions

When do females resist?

Male-initiated sexual interactions were met with female resistance in 74.3 % [75 cases of 101] at Suaq and 32.5% [66 cases of 203 total] at Tuanan, respectively. There was a significant interaction between female parity and resistance relative to time to conception (β=1.925±0.605, OR=6.85, z=3.181, P=0.001): Nulliparous females' resistance declined as conception approached, whereas that of parous females did not (Figure 17). Female resistance was more likely when the male was unflanged than flanged (β=-1.641±0.612, OR=0.19, z=-2.681, P=0.007). We could not test the interaction between male morph and female parity due to a lack of data (suppl. mat. Stable 24). The probability of female resistance increased with increasing local fruit availability (β=0.381±0.182, OR=1.46, z=2.096, P=0.04), but did not differ between the two study sites. We could not find any evidence that either the total number of copulations observed during a dyadic association or the duration of the association was related to female resistance behaviour (Table 11).

Table 11 Female resistance to male mating initiation: Binomial GLMM output for the probability of female resistance behaviour given that there was a male mating attempt/a male initiated copulation ($\chi^2_{2,10}$ = 45.614, P<0.0001, pseudo-R^2=0.55, N=304 sexual interactions of 18 different females [random intercept] and 62 males [no random intercept]). (Note: z = continuous values were z-transformed prior to the analysis to facilitate model convergence)

	Estimate	SE	Odd's ratio	z value	P value
Intercept	-0.604	1.054			
Site (Suaq vs. Tuanan)	-0.734	0.877	0.48	-0.836	0.403
Female parity (nulliparous vs. parous)	1.862	0.604	6.44	3.085	0.002
z Time to (known) conception (y)	-2.018	0.575	0.13	-3.509	<0.001
Male morph (unflanged vs. flanged)	-1.641	0.612	0.19	**-2.681**	**0.007**
z Dyadic association duration	-0.099	0.261	0.91	-0.379	0.705
Number of copulations during dyadic association	-0.068	0.129	0.93	-0.524	0.600
z Fruit Availability Index	0.381	0.182	1.46	**2.096**	**0.036**
Female parity : z Time to conception	1.925	0.605	6.85	**3.181**	**0.001**

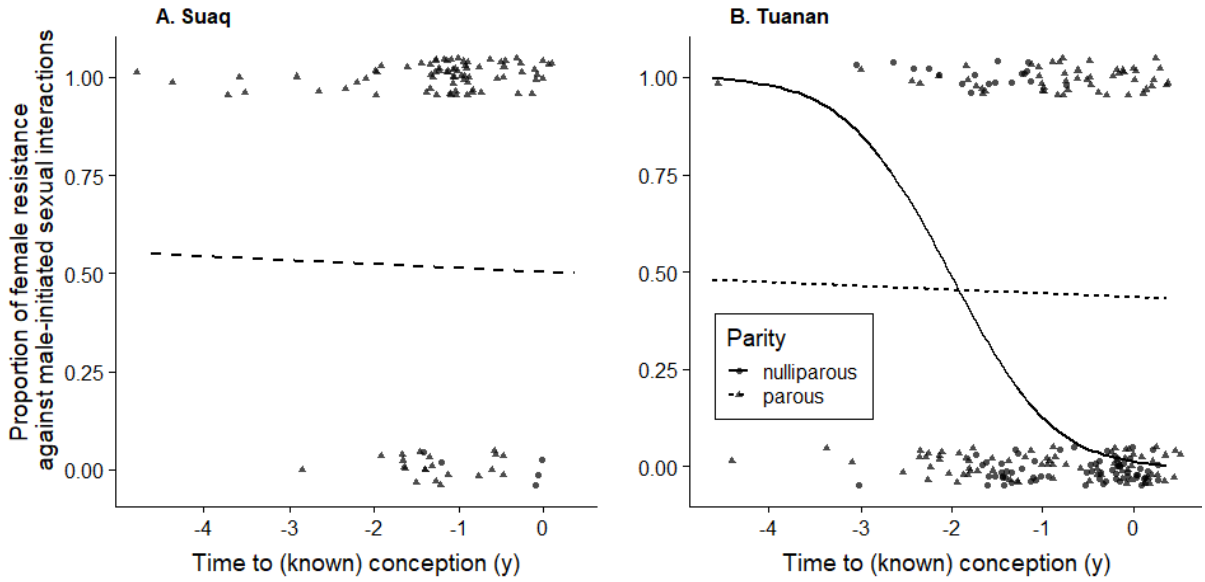

Figure 17 Probability of female resistance to male-initiated sexual interactions by study site (left: Suaq; right: Tuanan) depending on female parity and the time to known conception. The lines (dashed: parous; solid: nulliparous) show the model predictions (Table 11). The dots (round: nulliparous; triangles: parous) illustrate the raw data (jitter function to make them visible around 0 and 1). The predictions for nulliparous females are not depicted in the Suaq population, because only few copulations were observed mostly ranging from [-1, 0] years prior to conception.

When is female resistance successful?

Males achieved intromission despite female resistance in 81.6 % of the 141 resisted interactions. Thus, female resistance was mostly unsuccessful: Males did not achieve intromission in only 9.3 % at Suaq and 28.8 % at Tuanan when females resisted. The low proportion of successful resistance in our data set (N=26) made it difficult to account for all possible responsible factors quantitatively. We could not find any pattern of successful female resistance depending on male morph, female parity, time to conception, or interruptions by other males (suppl. mat. Stable 29). Overall, other males interfered with female-resisted sexual interactions in 10.6 % of all resisted sexual interactions, but this interference never involved any physical contact between the two males. Only 3 out of 26 cases of successful female resistance involved another male interrupting the interaction. Sexual interactions were never observed to be interrupted by other females at either of the two study sites.

Duration of sexual interactions depending on female resistance

The duration of body contact between a male and a female varied with the type of sexual interaction and the latter did improve the model fit for body contact duration significantly ($\chi^2_{8,12}$=93.18, P<0.0001) (suppl. mat. Stable 30). Body contact lasted longer when females resisted copulations than when they did not resist (β =-0.223±0.073, t=-3.054, P=0.002) (suppl. mat. Sfigure 13). The model did not further improve when we added the interaction between sexual interaction and study site ($\chi^2_{12,16}$=8.03, P=0.09). Intromission breaks were less likely to occur when females did not resist copulations (β= -0.860±0.430, OR= 0.42, z=-1.998, P=0.05) and a trend indicated that intromission breaks were less likely during proceptive than resisted copulations (β = -1.236±0.676, OR=0.29, z=-1.828, P=0.07), while accounting for the increased probability of intromission breaks with increasing interaction duration (β=0.111±0.037, OR=1.12, z=3.002, P=0.003). The full model for intromission breaks was significantly better than the null model ($\chi^2_{3,5}$=20.181, P<0.0001, N=170 of 29 female identities).

When are females proceptive?

Female proceptive behaviour, including the initiation of body contact and positioning herself to facilitate intromission, was rarely observed during the study period of 15 years at Tuanan (N=10) and 10 years at Suaq (N=23), respectively (suppl. mat. Stable 24). At Suaq, the majority of the female proceptive behaviour was directed towards flanged males (91.3% [21 of 23 observations]). The dominant flanged male at Suaq between 2007 and 2014, received 82.6% [19 of 23 observations] of all observed female proceptive behaviour. Only 2 of 23 female proceptive occurrences were directed towards another flanged male, after the dominant male has lost his status in 2014, and 2 towards an unflanged male. At Tuanan, parous females were more proceptive towards flanged males (4 of 5 observations), while nulliparous females showed proceptivity more towards unflanged males (4 of 5 observations). Female proceptive sexual behaviour was observed closer to conception (ranging from 1.4 years prior to and up to the estimated time of conception) than other sexual interactions. No female proceptive sexual interactions were observed during pregnancy (Figure 14, Figure 16). Most of the female proceptive interactions resulted in intromission, with the exception of 3 dyads (for further details see suppl. mat.).

Discussion

Both parous and nulliparous orang-utan females exhibit an exceptionally long period of sexual activity, starting at least 2-3 years prior to conception, although there appears to be large variability between females which is not just linked to sampling effort or study site and species (Figure 14). This extended period of sexual activity leads to highly promiscuous mating patterns. Orang-utan females do not exhibit any visual signal of fertility (Nunn, 1999; Zinner et al., 2004), and ovulation appears to be concealed from males (Knott et al., 2010; Nadler, 1981). Accordingly, males initiated the vast majority of sexual interactions, even at a near-zero chance of fertilization, and thus, are the immediate driver of the observed extended, promiscuous female sexuality. Although some infant ages were estimated in our

study (Table 8) and failed pregnancies may have gone undetected because of the scarce endocrine data, we can be confident that the onset of sexual interactions was well before conception and likely during periods of lactational infertility. First, almost all females were observed in sexual interactions well before one year prior to estimated conception (Figure 14). Second, failed pregnancies are unlikely to have affected our conclusions either, since it would merely produce more noise around conception, but not affect the broader pattern of the extended mating period.

Male rule of thumb

Although not directly related to the presence of endocrine indicators of ovarian cycling (suppl. mat.), mating rates still increased as conception approached, indicating that males had some, if limited, information about a female's likelihood of conception. Males not only initiated most sexual interactions, even during early stages of pregnancy and other times when females were highly unlikely to conceive, but were previously reported to also generally maintain associations with females (chapter 3). Because males presumably also incur costs from mating and associating with females, they likely follow a set of decision rules when to copulate with a female. First, males likely use the size of a female's dependent offspring as a rule of thumb to assess her reproductive state. The dependent infant appears to act as a cue similar to a graded signal, at least for parous females and at a far cruder time scale, without any additional physiological costs of a sexual swelling (Nunn, 1999).

Second, males likely rely on female proceptive behaviour. Female proceptive behaviour is rare, however, (this study; O'Connell et al., 2019; Schürmann, 1982) and very selectively directed at (mostly) flanged males. Female proceptivity has been linked to the periovulatory period (Knott et al., 2010). Although we could not link our behavioural data with endocrine data, also in our data set female proceptivity occurred closer to conception than male-initiated sexual interactions, suggesting a link to fertile periods. As reported in previous studies, we observed most female proceptive behaviour directed at flanged males. Yet, also unflanged males received a few female proceptive acts mostly by nulliparous females, who were reported to display different mating strategies than parous females (O'Connell et al., 2019). Non-preferred males who cannot rely on being approached by females perhaps eavesdrop on female behaviour towards other males to assess female reproductive state, which may explain the prolonged, male-maintained associations (chapter 3). Proceptive behaviour may therefore signal fertility to selected males, whereas it remains to be understood how accurate such behavioural cue would be.

Third, female parity may play a role for flanged males' decision rules, but less for unflanged males. Unflanged male mating preference does not appear to distinguish between nulliparous and parous females, who experienced similar rates of male-initiated copulations. These rates were best explained by the association time with unflanged males, but not by the association time with flanged males. Our findings conform with the suggestion that consorting nulliparous females is one aspect of the alternative reproductive tactics of unflanged males, which may allow them to gain some siring success with nulliparous females (Utami Atmoko et al., 2009a, 2002) who are less preferred by flanged males due to the generally low likelihood of conception (MacKinnon, 1974; O'Connell et al., 2019; Schürmann, 1982, 1981; Schürmann and van Hooff, 1986). Flanged males reportedly even occasionally refuse female proceptive initiations, especially by nulliparous females (for a review across different study sites see O'Connell et al., 2019) and hence, might be somewhat selective. In our data set, however, the dominant flanged male at Suaq refused proceptive attempts by a parous female even several times. Such observations are puzzling and indicate that males integrate multiple cues to decide when to mate.

Fourth, we cannot exclude that olfactory cues convey information to orang-utan males about female reproductive state, as suggested in other primates (review: Drea, 2015; humans: Lobmaier et al., 2018; chimpanzees: Matsumoto-Oda et al., 2003). Especially unflanged males frequently investigate the genitals of females with infants of any age (Knott et al., 2010; Schürmann, 1982; chapter 3). At present, it is unknown which information males gain from these investigations and how they relate to sexual interactions. In any case, regarding the observed mating pattern in this study, it appears unlikely that olfactory cues convey accurate information on the ovulatory state of females. To sum up, depending on

their morph and dominance status, orang-utan males likely use a variety of more or less inaccurate cues for female reproductive state, including the size of the females' dependent offspring, her proceptive behaviour and parity status.

Polyandrous mating for paternity confusion?

Female orang-utans were observed to mate highly promiscuously over an extended period. Because we observed individual females on average only on 30±SE 8 focal follow days in the year prior to conception (Figure 14), i.e. not even 10% of their active time, on average female's actual number of both mating partners and copulations per conception is likely multiple times larger than reported in our study (suppl. mat.). There must be a reason why females do not reliably signal fertility to males just around the window of ovulation, which would allow them to avoid costly male-maintained associations and reduce their vulnerability to forced copulations during periods of lactational infertility. The absence of fertility advertisement appears paradoxical, especially when considering that orang-utan females advertise non-availability during pregnancy with small labial swellings (Galdikas, 1981; Schultz, 1938). One explanation for the concealed ovulation of orang-utan females may be the need for extended mating periods to achieve paternity confusion and counteract the risk of infanticide (Hrdy, 1979; van Schaik and Janson, 2000). Infanticide qualifies as a viable male strategy if i) he is not the sire of the infant, ii) the female returns faster to fertility when losing the infant than when weaning it and, iii) the male has mating access to the female after killing her dependent offspring (Hrdy, 1979; van Schaik, 2000). Infanticide has never been directly observed in wild orang-utans (but one case in captivity: Mallinson, 1984) and males have not been documented to exhibit any aggressive behaviour towards infants (Beaudrot et al., 2009; Marzec et al., 2016). Nevertheless, orang-utan infants have been reported to disappear for unknown reasons (Knott et al., 2019; MvN, CvS and C. Schuppli, pers.comm.) and females became fertile within months after they lost their infants (Knott et al., 2019; van Noordwijk et al., 2018). Given the relatively short time to conception after infant loss, infanticidal males, if dominant and in good condition, could potentially gain reliable the access to a particular female despite the high costs of association (van Schaik et al., 2009b). The absence of direct observations is a recurring issue, when studying sexually selected infanticide (Hrdy, 1979; Hrdy et al., 1994; van Schaik and Janson, 2000). If females win the informational arms race with their efficient counterstrategies (e.g. bonobos: Hohmann et al., 2019), infanticide may not present a viable strategy for males despite life history traits favouring infanticide as a male strategy (i.e. females with high lactation to gestation ratio). On account of the few infants female orang-utans have over a lifetime (van Noordwijk et al., 2018; Wich et al., 2009), the loss of an infant after potentially several years of investment implies a considerable fitness loss (van Noordwijk et al., 2013; van Noordwijk and van Schaik, 2005).

Orang-utan females display the classic female counterstrategies to infanticide (van Schaik, 2016; van Schaik et al., 2004, 1999). In the absence of continued associations with a protector (Mesnick, 1997; van Schaik and Kappeler, 1997; Wrangham, 1979), the risk of fluidity in male dominance relationships and long absence of males from a females' home range (Utami Atmoko et al., 2009b), females may heavily rely on their extended sexuality and polyandrous mating to confuse paternities and to effectively reduce the risk of infanticide (e.g. bears: Bellemain et al., 2006) at the cost of the exposure to frequent sexual harassment. First, they exhibit concealed ovulation, which makes them attractive to males over an extremely long period and leads to multiple copulations with multiple males (of all ranks) per conception, as well as early-pregnancy copulations. Second, female orang-utans do approach and signal receptivity with their proceptive behaviour towards dominant flanged males, presumably around the time of ovulation (Fox, 1998, 2002; Mitra Setia and van Schaik, 2007; Schürmann, 1981; Spillmann et al., 2010). These are exactly the males who happen to pose the highest infanticide threat, if without high paternity certainty (Clarke et al., 2009), but are the best protectors when with a high estimate of paternity (Fox, 2002; Mesnick, 1997; van Schaik and Kappeler, 1997).

Moreover, orang-utan females reportedly adjust their mating tactics to the stability of the male dominance relationships. In (West) Sumatran populations, where male dominance relationships appear more stable (Dunkel et al., 2013), female preference is more pronounced towards the dominant flanged

male (Suaq: this study; Fox, 1998, 2002; Ketambe: Mitra Setia and van Schaik, 2007). For example, female promiscuity increased when the dominant flanged male in Ketambe was deposed (Utami Atmoko and Setia, 1995) and paternity was distributed among many different males (Utami Atmoko et al., 2009a, 2002). Besides the clear female preference for the dominant male at Suaq, we could not find any site differences between Suaq and Tuanan concerning mating patterns. This may be the result of the unstable period at Suaq between 2014 and 2018 (e.g. Lisa with exceedingly high mating rates during this period). In Bornean populations, where male dominance relationships are less stable (Dunkel et al., 2013; Spillmann et al., 2017), females have been reported to hide from males (Knott et al., 2018; Scott et al., 2019; MvN, unpubl.), which may function not only to avoid possible costly associations (chapter 3), but also to prevent both sexual harassment and infanticide. Some of the few known cases of infant disappearance coincided with the displacement of the dominant male in Sumatran populations (CvS, C. Schuppli, pers. comm.) and the influx of new males, who have no mating history with the local females in Bornean populations (Knott et al., 2019; MvN pers. comm.). Although the reason for the infants' disappearance is unknown in all the cases, we hypothesize that there may be a residual risk of sexually selected infanticide in orang-utans, when male dominance relationships are unstable, just as observed in other species and predicted by theoretical approaches (van Schaik et al., 2004; van Schaik and Janson, 2000). If such a residual risk of infanticide persists, the current conservation practice of translocating individual males from disturbed habitat into existing orang-utan populations may be even more detrimental.

The large between-female variability in terms of mating partner and copulation number is surprising and may be the result of either male and female reproductive strategies, or both (Emery-Thompson and Alvarado, 2012). Specifically, variation may result from both the interaction of the prevailing male dominance relationships (as discussed above) and individual female condition and tactics. There is evidence for both female-female competition (Knott et al., 2008; Marzec et al., 2016; van Noordwijk et al., 2012) and varying female physiological condition in orang-utans (Knott et al., 2009), which may lead to between-individual and temporal variation in female reproductive strategies. In other primate species higher individual female promiscuity has largely been attributed to higher female rank and better condition, which allowed females to engage in prolonged mating periods (and increased polyandrous mating) (mouse lemurs: Huchard et al., 2011; chimpanzees: Stumpf and Boesch, 2005). The variability in female mating activity may therefore be related to a female's perceived habitat quality. Perhaps because female orang-utans trade-off the high energetic costs of association linked to copulating at higher rates to reduce of the risk of infanticide against more intensive hiding behaviour during early lactation. Alternatively, the variability is a male-driven result caused by frequent sexual coercion, indicating that the males have the upper hand in the arms race and the polyandrous mating is the result of convenience polyandry. Unfortunately, it may take another few years of behavioural and endocrine data to reveal in how far individual orang-utan females ultimately benefit from polyandrous mating, in terms of reproductive success. We need population comparisons which include female reproductive state, male dominance relationship stability and siring success to further understand how female reproductive strategies vary temporally within and across study sites with varying ecological backgrounds.

Why do females resist?

Female resistance behaviour may appear puzzling, as it also occurs during periods when a female is highly unlikely to conceive (up to 4 – 5 years prior to conception). This sexual conflict over mating has largely been attributed to male quality (Fox, 1998; Knott et al., 2010) and female ovulatory state (Knott et al., 2010; Nadler, 1981). It appears that nulliparous female resistance settles on periods when females are highly unlikely to be fertile and decreases as conception approaches. This is in accordance with a recent study stating that nulliparous females likely initially learn how to behave around males (O'Connell et al., 2019), which may also explain the decrease of resistance as conception approaches in our study. In contrast, the decrease in resistance behaviour is far less pronounced in parous females. This negative female choice over an extended period may serve paternity confusion (also see Knott et al., 2010). If females would only resist to non-preferred males when likely to conceive, they

would give away their ovarian status behaviourally. Resisted copulations impose energetic costs on females, as they last longer than non-resisted copulations both at Tuanan and Suaq (but see: Knott et al., 2010). Thus, resistance involves extra effort for the female and therefore is expected to bring some immediate or delayed benefits (Parker, 1979). First, female resistance can be successful (20% of cases) and the male stops his copulation attempt. Thus, female resistance directly and successfully signals non-availability to the male. Second, males may be less likely to ejaculate if females resist. Resistance led to repeated intromission breaks and thereby intromission duration and ejaculation probability is likely reduced (eg. rodents: Wilson et al., 1965). Visibility constraints (because of the dense canopy) make it difficult to reliably assess if orang-utan males ejaculated during sexual interactions even when video recordings are available. Orang-utans have uniquely long copulations, also when females cooperate, compared to other great apes (for review: Dixson, 2009). If female cooperation is necessary to some degree for a male to ejaculate or to facilitate fertilization, female resistance may function to avoid undesired fertilization. Third, female resistance may attract male competitors and thus, allow the female to get rid of harassing males (elephant seals: Cox and Le Boeuf, 1977; fowls: Løvlie et al., 2014; elephants: Moss, 1983). Although, orang-utan males interfered rarely directly during sexual interactions, they may contribute to end an involuntary association (van Noordwijk and van Schaik, 2009). All in all, female resistance may have various, not mutually exclusive immediate benefits for the female, which remain to be fully understood.

Conclusions

Female orang-utans combine concealed ovulation and a hyper-extended period of mating per conception. Males likely take the size of the infant as a rule of thumb for female reproductive state and, accordingly, may perceive females as attractive already 2 - 3 years prior to the actual conception. Therefore, sexual conflict in orang-utans may not only arise due to the males' identity or morph (Utami Atmoko and van Hooff, 2004), but also about the timing when to mate (also see Knott et al., 2010). Ultimately, orang-utan females' extended sexuality and the resulting polyandrous mating may represent the best possible anti-infanticide strategy for females vulnerable to sexual coercion (van Schaik et al., 2004) given the costs of association (chapter 3), which prevents bonobo-like mating intensity and paternity confusion (Hohmann and Fruth, 2003; Douglas et al., 2016).

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Chapter 5: Context of Sexual Coercion in Orang-utans – when do male and female mating interests collide?

Julia A. Kunz[1], Guilhem J. Duvot, Erik P. Willems[1], Maria A. van Noordwijk[1], Julia Stickelberger[1], Brigitte Spillmann[1], Sri Suci Utami Atmoko[2], Carel P. van Schaik[1]

1) Department of Anthropology, University of Zurich, Switzerland
2) Faculty of Biology and Primates Research Center, Universitas Nasional, Indonesia

Abstract

In orang-utans the frequent occurrence of sexual coercion, in the form of forced copulations, has largely been attributed to alternative reproductive strategies of particular males in combination with the concealed ovulation of females. So far, however, the immediate contextual variables leading to forced copulations have rarely been examined. Here, we did this for both resisted and non-resisted copulations. We compared two study populations, Suaq (*Pongo abelii,* Sumatra) and Tuanan (*Pongo pygmaeus wurmbii,* Borneo), which differ in their socio-ecology, and assessed the relative importance of female reproductive state, male morph (unflanged or flanged), measures of male-male competition, male-female relationship and ecological factors on the occurrence of both resisted and voluntary copulations.

Even though female reproductive state and male morph explained some female resistance, predictors were also related to male-male competition. Female resistance was more likely towards subordinate males who were displaced from proximity to the female during the dyadic association. Females were also less likely to resist copulations of males, who had just displaced another male. The dyadic familiarity of male and female did not affect the probability of copulation, whereas the presence of additional flanged males increased the probability of female resistance. Moreover, both the latency to the arrival of another male and to the end of the association after sexual interactions was shorter if there was female resistance. We conclude that female resistance in orang-utans is highly dependent on the vicinity of more dominant males. While males follow a "*now-or-never*" strategy and force copulations when at risk of losing access to a female, female resistance follows a "*not-you-now"* pattern, which is ultimately congruent with an infanticide avoidance strategy.

Keywords: mating tactics, male competition, female leverage, infanticide avoidance

Introduction

A high, male-biased operational sex ratio may lead to female choice, male-male competition and sexual conflict (Darwin, 1871; Parker, 1979). These three mechanisms of sexual selection are not mutually exclusive, and hence may be difficult to disentangle. In some species, sexual conflict is expressed behaviourally as sexual coercion (Pradhan and van Schaik, 2009), which can take different forms, such as harassment, intimidation/punishment and forced copulations (Clutton-Brock and Parker, 1995). Smuts and Smuts (1993) defined it as „*…use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female"*.

Orang-utans have a dispersed mating system, and besides humans (Emery-Thompson, 2009; Thornhill and Palmer, 2001; Thornhill and Thornhill, 1983), orang-utans are the only primate species where forced copulations are frequently reported (Galdikas, 1985a; Knott et al., 2010; Knott and Kahlenberg, 2007; Mitani, 1985a; Schürmann and van Hooff, 1986; Utami Atmoko et al., 2009a). The long inter-birth intervals of 6 to 9 years (van Noordwijk et al., 2018) combined with the concealed ovulation of females (Knott et al., 2010; Nadler, 1981), the large sexual dimorphism (Leigh and Shea, 1995), and the semi-solitary lifestyle (Rijksen, 1978) make female orang-utans vulnerable to male coercion. Yet, apparent physical injuries resulting from these forced copulations are absent (Fox, 1998; MacKinnon, 1974; Rijksen, 1978), suggesting that the males use just as much force as necessary to overcome female resistance and achieve intromission. Accordingly, forced copulations have increasingly been defined by the presence of female resistance behaviour rather than the male's use of force (Fox, 1998; Knott et al., 2010; Utami Atmoko, 2000). Thus, female-resisted copulations are the expression of sexual conflict rather than the expression of a particular male phenotype (Emery-Thompson and Alvarado, 2012).

Originally, forced copulations in orang-utans were seen as an expression of the alternative reproductive tactics (Gross, 1996) of unflanged males, who lack secondary sexual characteristics (SSCs) including cheek pads, laryngeal sac, the emission of long-calls and increased body size (Galdikas, 1985b; MacKinnon, 1974; Rijksen, 1978; Utami Atmoko and van Hooff, 2004). Although able to reproduce (Dahl et al., 1993; Goossens et al., 2006; Utami Atmoko et al., 2002), they would have to coerce females into mating, thus following a "*best-of-a-bad-job*" mating strategy, because unflanged males are generally not preferred by females. However, unflanged males also have unforced copulations and thus coercion is neither an "unflanged-default" nor an individual male trait (chapter 2). Rather unflanged males' mating interests are more likely to conflict with female interests, because they associate and try to copulate more frequently at times when females are highly unlikely to be fertile.

Flanged males, who have fully developed SSCs and emit long-calls, are approached by receptive females (Mitra Setia and van Schaik 2007; Spillmann et al. 2010; but see: Mitani 1985b) and they have more female-proceptive copulations than unflanged males (Fox, 1998; Knott et al., 2010). Nonetheless, even flanged males occasionally force copulations (Knott, 2009). Considerable variation across study sites concerning the duration of developmental arrest of SSCs (Delgado and van Schaik, 2000; Dunkel et al., 2013) and morph-specific coercion rates (Knott, 2009; Knott and Kahlenberg, 2007; Utami Atmoko et al., 2009a) have been reported. In Bornean populations the developmental arrest of SSCs is less pronounced (Delgado and van Schaik, 2000; Dunkel et al., 2013) leading to a higher flanged to unflanged male ratio (Dunkel et al., 2013), more confrontational assessment among flanged males and unstable male dominance relationships (Spillmann et al., 2017). Correspondingly, direct contest competition over access to females is high among flanged males in Bornean populations (Dunkel et al., 2013; Utami Atmoko et al., 2009b) and overall higher coercion rates for flanged males have been reported there (Knott, 2009; Utami Atmoko et al., 2009a). All in all, these observations therefore again

support the idea that coercion is a variable and highly context-dependent mating tactic, rather than a morph-specific strategy or an individual male trait.

This perspective suggests that efforts to understand the function of forced copulations should focus on female resistance. This was found to depend on her reproductive history, i.e. parity, and her current ovulatory state (Fox, 1998; Knott et al., 2010; O'Connell et al., 2019). While nulliparous females resist less as conception approaches, parous females' resistance rates do not change, although overall male-initiated sexual interactions increase with approaching conception (chapter 4). Male orang-utans likely do not have any reliable indicator of female fertility (sensu Nunn, 1999), apart from the size of the females' dependent offspring and female proceptive behaviour (Fox, 1998), and accordingly male sexual interest may restart years prior to conception (chapter 4). Because female resistance behaviour leads to longer interactions (chapter 4; but not at all study sites: Knott et al., 2010) and is therefore costly for females, the function of resistance behaviour during periods when females are highly unlikely to conceive is puzzling. It may reflect both a residual chance to be inseminated by a non-preferred male regarding the variable inter-birth intervals (van Noordwijk et al., 2018; Wich et al., 2009) and be part of a paternity confusion strategy (Knott et al., 2010). All in all, not only the male decision to mate, but also the female's resulting resistance varies with the immediate context.

The function of female resistance may be linked to attracting more preferred males (Fox, 2002; Mesnick, 1997). Orang-utan female resistance, which manifests by the female actively trying to avoid intromission by repeatedly attempting to move away and struggling against the male, is often accompanied by loud vocalizations (Fox, 1998; Knott et al., 2010; Utami Atmoko, 2000). In non-primates, female resistance has been found to lead to the displacement of the harassing male by another more dominant male (elephant seals: Cox and Le Boeuf, 1977; fowls: Løvlie et al., 2014; elephants: Moss, 1983). Such displacements are likely brought about by female vocalizations. In primates, copulation calls by females similarly function to increase male competition (chimpanzees: Fallon et al., 2016; primates in general: Pradhan et al., 2006; van Schaik et al., 1999), and their production is context-dependent (chimpanzees: Townsend et al., 2008). In orang-utans, male-male aggression is more likely in the presence of sexually active females (Spillmann, 2017; Spillmann et al., 2017; Utami Atmoko, 2000; Utami Atmoko et al., 2009b) and orang-utan females have been reported to exert some leverage over males in the context of food transfers through loud vocal protests (van Noordwijk and van Schaik, 2009).

The avoidance of mating with non-preferred males, if it does not reflect selection on male intrinsic viability (Andersson, 1994), is plausibly linked to infanticide avoidance (Hrdy, 1979). Orang-utans have very slow life histories (van Noordwijk et al., 2018; Wich et al., 2009), which make them vulnerable to the conception-hastening effect of infant loss (van Schaik, 2000). Although infanticide by males has never been observed, indirect evidence for it has been published (Knott et al., 2019, 2010), and various behaviour patterns are consistent with females' responses to unfamiliar males (Scott et al., 2019). Infanticide avoidance has clear implications for female reproductive physiology and mating strategies in potentially promiscuous species (Hrdy and Whitten, 1987; van Schaik et al., 1999). As to reproductive physiology, we expect long follicular phases to the ovarian cycle and in some cases, concealed ovulation (van Schaik et al., 2000), as in orang-utans (Nadler, 1981). Behaviourally, females are expected to be selectively promiscuous to achieve the optimal balance of paternity assessments among the males in the neighbourhood, including protection by likely fathers and refraining from attack by unlikely ones (van Schaik et al., 2004). This manipulation may include mating during times when conception is unlikely or impossible as reported from orang-utans (Knott et al., 2010) and the avoidance of mating with subordinates in the presence of dominant males (van Schaik et al., 2004). Here, we investigate these immediate consequences of female-resisted sexual interactions and assess if female resistance during sexual interactions relates to the presence and arrival of other males.

Another possible, non-exclusive function of female resistance must also be considered. Some previous studies on orang-utan sociality suggested the presence of long-term male-female relationships (Mitra Setia et al., 2009; Utami Atmoko et al., 2009a). In other catarrhine primates, male-female friendships have been linked to indirect paternal care, such as protection from infanticide (Palombit, 2000; chacma baboons: Baniel et al., 2016; Moscovice et al., 2010; chimpanzees: Murray et al., 2016; olive baboons: Städele et al., 2019) or to male mating effort (chimpanzees: Langergraber et al., 2013; olive baboons: Städele et al., 2019). Both functions of friendships appear unlikely in orang-utans. First, there is no paternal care besides lactating females maintaining ear-shot associations with dominant flanged males to avoid (potentially infanticidal) harassing males (Fox, 2002; Mitra Setia and van Schaik, 2007). Second, there is little behavioural evidence for long lasting affiliative male-female relationships. Associations are rare, and almost always asymmetric, i.e. male-initiated and male-maintained (chapter 3). In fact, females incur foraging costs from these associations (chapter 3) and have been reported to only actively approach dominant, flanged males around conception (Fox, 1998; Knott et al., 2010; Spillmann et al., 2010). Finally, long-term relationships with other, subordinate males are precluded, because the preference of both lactating and receptive females is tightly linked to current male dominance relationships (Utami Atmoko and Setia, 1995), congruent with female infanticide avoidance strategies (Knott et al., 2019, 2010; Scott et al., 2019) and consistent with the skew in paternities (Banes et al., 2015; Goossens et al., 2006; Tajima et al., 2018; but see Utami Atmoko et al., 2002). Nevertheless, it remains to be tested if dyad composition explains some variation in the observed sexual conflict patterns and if high dyadic association frequency relates to mating and/or coercion frequency.

Aim of the study

The aim of the present study was to revisit the paradox of female-resisted copulations in orang-utans with the largest data set collected so far on this taxon, in two different orang-utan populations, at Suaq on Sumatra (*Pongo abelii*), and at Tuanan on Borneo (*Pongo pygmaeus wurmbii*). Specifically, as a further evaluation of the infanticide avoidance hypothesis, we aim to understand the interaction between female and male preferences that lead to resisted copulations and identify the exact contexts in which males force and females resist copulations. We therefore controlled for previously known characteristics of the males that force and of the females that resist copulations – male morph and female reproductive state – and tested the relative importance of male competition and dyad composition on the occurrence of sexual interactions in association dyads (Table 12). Particularly, we assessed if the probability of either resisted or non-resisted copulations was affected by the presence of additional males throughout the association, actual displacement events by a competitor, association length, or the total time spent in a particular dyad. To test whether female resistance is context-dependent and correlates with measures of male-male competition, we also evaluated the immediately subsequent events, including the presence and consecutive arrival of other individuals and association maintenance following sexual interactions.

Methods

Study sites and study subjects

Long-term behavioural data of two study sites were analysed: Tuanan, Mawas Reserve, Central Kalimantan, Indonesia (02°15'S; 114°44'E) and Suaq, Gunung Leuser National Park, South Aceh, Indonesia (03°02'N; 97°25'E). At both study sites data was collected by well-trained observers. At Tuanan data was collected during 15 years (July 2003 to July 2018); we could evaluate a total of over 34 500 focal follows hours on parous females, over 6 500 hours on nulliparous females, over 18 200 flanged and over 6 700 unflanged male focal follow hours. At Suaq, data collection lasted 11 years (June

2007 to March 2018); we analysed more than 6 700 focal follow hours on parous females, 1 700 hours on nulliparous females and over 2 300 flanged and over 1 300 unflanged male focal follow hours.

The subjects were individually recognized thanks to the long-term data collection effort. We identified individuals by both visual inspection of almost daily photographs during follows, as well as genetic verification (Arora et al., 2012; M. Krützen and C. Ackermann, pers.comm.). The identities of the individuals were regularly checked by several independent observers. Because at both study sites, males may not be seen for several months or even years (Dunkel et al., 2013; Spillmann et al., 2017; Utami Atmoko et al., 2009b), the identification of males was difficult, especially for transient males who were rarely seen in the study area. We used a conservative approach and new male identities were assumed if several trained observers did not unambiguously identify the male. The large number of different males in the analyses may therefore be a slight overestimation of the actual number of different males. Because female orang-utans are philopatric (van Noordwijk et al., 2012), exhibit a high site fidelity (Ashbury et al., in rev.), and are therefore more regularly observed, they could be reliably identified. The age of the dependent offspring was either known or estimated to the closest year (cf. van Noordwijk et al., 2018) and was taken as a proxy for the reproductive state of parous females (Fox, 1998). Pregnancy was detected either using urine quick tests (Knott et al., 2010) and/or by back-dating 245 days from the known or estimated date of birth (Graham, 1988).

Behavioural data

Focal animal behavioural data was collected according to an established protocol (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). Association partners (all individuals within 50m of the focal animal) were noted at 2-min intervals. Orang-utans most likely can keep track of each other's presence at larger distances than 50 metres (van Noordwijk et al., 2012, as seen in mother-juvenile ranging patterns and selective female-female encounters: 2009) and hence, short-term interruptions of the within 50 metres distance are likely not independent of each other. Thus, a particular male-female association was counted as lasting over several days, if the association partners did not separate for more than 1 full-day focal follow out of the 50 m proximity. Correspondingly, an association dyad unit may also comprise periods when the association partners were at a distance of more than 50m, but returned to within 50m later (Table 12). We took all-occurrence data on sexual interactions and the identity of the involved individuals (Altmann, 1974). Because male-female associations and especially sexual interactions are relatively rare (Suaq: 159 copulations during > 12 000 observation hours; Tuanan: 313 during > 65 000 hrs), data from both adult male and female focal follows were combined in the analyses. We distinguished between copulations, when the male achieved intromission, and failed attempts to achieve intromission. Sexual interactions, which comprises both copulations and attempts, were subdivided into *female-resisted* and *non-resisted*. Female *passive* and *proceptive* sexual interactions were considered as *non-resisted* in the analyses, whereas we labelled as *resisted* any sign of female resistance throughout the interaction, including *"(repeated) attempt(s) to move away from the male, obstructing the male's attempt to position the female for intromission, slapping and biting the male to evade intromission, and is often, but not necessarily, accompanied by the female's squeal or scream vocalizations"* (chapter 4). Furthermore, we included data on the rare occurrence of coercive mate guarding by males in the population of Tuanan (N=15): A male engaged in coercive hand-holding outside of the context of obvious sexual action, i.e. he held one of the extremities (usually wrist or ankle) of females up to several hours and thereby restrained them from moving away (for details: van Schaik et al., 2006).

Table 12 Variables, their definitions and predictions how they may affect the occurrence of sexual interactions, both with and without female resistance, on the level of male-female associations.

	Variable	Definition	Predictions
Female reproductive state	*Parity* *(nulliparous vs. parous)*	Parous females have either known dependent offspring or are known to having had an offspring previously. Nulliparous females or adolescent females are known to be sexually active, but have not yet given birth to their first offspring.	Nulliparous females experience a long period of subfecundity[1] and were reported to be less preferred by flanged males[2]. Accordingly, they follow different mating strategies than parous females[3].
	Age of dependent infant (y)	The known or estimated age of the dependent offspring of (both primi- and multi-) parous females (to the closest year).	Both resisted and non-resisted copulations increase with the age of the dependent offspring, i.e. as conception approaches[3]
Male	*Male morph* *(unflanged vs. flanged)*	*Flanged males* have fully grown SSC, including cheek pads, laryngeal sac, emission of long-calls). *Unflanged males* lack the secondary sexual characteristics (SSC) but are sexually active, adult males.	Unflanged males both exhibit higher copulation and coercion rates than flanged males. Flanged males are generally preferred by fertile females and accordingly experience less female resistance. These patterns may differ between study sites.
Male-male competition (and female choice)	*Number of other males*	The total count of additional males observed in association(<50m) with a particular female during all the days of a specific dyadic male-female association. The males were not necessarily simultaneously <50m of the female. We chose this measure instead of only simultaneous male associations, because orang-utans likely perceive their presence on a larger distance than 50 metres.	If males perceive potential male-male competition and the risk of losing exclusive access to females, they may be more likely to copulate. Even though males hardly interrupt copulations with apparent female resistance[3], they may displace males from proximity to females. Thus, females may resist to attract potential protector males[4], when multiple males are in vicinity.
	Displacing another male *(no vs. yes)*	The male in the dyadic male-female association actively or passively displaced another male from being in closest proximity to the female in the course of the association. Note that the displaced male may stay in association, but at a larger distance to the female than the displacing male. We refer to displacing males as "*dominant"* males.	Dominant (flanged) males are preferred by fertile females[5,6] and thus, experience less female resistance. Females may resist less to dominant males, because they are good protectors and thus, reduce subsequent harassment[4].
	Displacement by another male (no vs. yes)	The male in the dyadic male-female association is (actively or passively) displaced by another male from the proximity to the female (see above). We refer to displaced males as "*subordinate"* males	Subordinate males may follow a "now-or-never" strategy, either when at the risk of displacement, i.e. there is another competitor arriving or when the displacing male is at a distance, they may try to sneak copulate with a female[6].
Male-Female relationship	*z Association duration (h)* *(continuous)*	The total active time a dyad was observed in association (from start to end time, excluding night hours and time when not <50m proximity)	Generally, males are responsible to maintain associations with females[7]. If males invest a long time to follow a female, they may also be more likely to copulate. Association time with males increases as females approach conception[7].
	z Dyadic familiarity *(continuous)*	The overall time a dyad was observed together throughout the entire study period, i.e. the association frequency of a specific dyad	1) The more time in association with a specific female, the more copulations are observed. 2) Association time with specific females allows males to monitor female sexuality and reproductive state, but does not necessarily increase his mating success/frequency.
Ecology	*z FAI* *(continuous)*	The local Fruit Availability Index was evaluated on monthly basis for both study sites (for details see "*Ecological Data"*)	Because both female reproductive physiology[8] and association patterns are known to vary with ecological factors[9], we expect an increased copulation rate during high FAI periods, especially if males perceive female fertility.
Population	*Site* *(Suaq vs. Tuanan)*	Suaq hosts reportedly the densest and most sociable Sumatran orang-utan population (*P. abelii*)[9,10]. At Tuanan the population density is lower, but still relatively high compared to other Bornean orang-utan populations (*P. pygmaeus*)[10]. The male developmental arrest of SSC is more pronounced and the male dominance relationships more stable at Suaq than Tuanan[11,12]	Females tend to experience more male-initiated copulations at Suaq than at Tuanan[3]. The association frequency is lower and accordingly, costs of association (and social interactions) higher at Tuanan than at Suaq[7,9,10]. Copulation probabilities within dyadic associations may be higher in the Suaq than the Tuanan population.

Footnotes:

z = indicates that a z-transformation was applied to the continuous variable prior to analysis

1: Knott, PhD-Thesis; 2: Schürmann 1981, 1982; Schürmann and van Hooff, 1986; O'Connell et al., 2019; 3: Chapter 4; 4: Fox, 2002; 5: Knott et al., 2010; 6: Fox, 1998; 7: Chapter 3; 8: Knott et al., 2009; 9: van Schaik, 1999; 10: Mitra Setia et al., 2009; 11: Dunkel et al., 2013; 12: Delgado and van Schaik, 2000.

Ecological data

At both study sites, fruit availability assessments were conducted on a monthly basis throughout the entire study period (Vogel et al., 2009). The Fruit Availability Index (FAI) reported here represents the percentage of trees with fruits over all surveyed trees (at Suaq ~1000 and at Tuanan ~1500 surveyed trees) (Harrison et al., 2010). Because at Suaq the FAI is generally higher than at Tuanan (Wich et al., 2011), the FAI was z-transformed within study site to have comparable values across the two sites (indicated by the "zFAI" in the results) and assess local FAI effects rather than between site differences.

Statistical analyses

All statistical analyses were conducted using R, version 3.5.2 (R Core Team, 2018). We formulated (generalized) linear mixed models ([G]LMMs) using the 'lme4' and 'lmerTest' packages (Bates et al., 2015; Kuznetsova et al., 2017). We checked for (multi)-collinearity of fixed factors using the Variance Inflation Factor (VIF < 2 for models excluding interaction terms) generated by the 'car' package (Fox and Weisberg, 2018). Further, we examined the models for influential cases and outliers. Additionally, we checked all the models with a Gaussian error distribution (LMM) for normality and homoscedasticity by the visual inspection of residual plots. We report the full models tested and the comparison to the null model, which contained the random intercepts only, based on likelihood ratio tests. The P value of 0.05 was used as cut-off value for significance. Further, the "pseudo-R^2" value (delta) for all the full models was calculated using the 'MuMIn' package (Barton, 2018). All figures were generated using the 'ggplot2' (Wickham, 2016) and 'cowplot' packages (Wilke, 2019).

Occurrence of copulations in dyadic associations

We examined the occurrence of copulations on the level of dyadic male-female associations from either male or female focal follows (or both). We checked the relative importance of indirect measures for the female reproductive state, male-male competition, male-female relationship, ecology and overall population differences (for definitions see Table 12). Because there is evidence for varying female mating strategies of parous and nulliparous females (O'Connell et al., 2019; Schürmann and van Hooff, 1986), we restricted the reported analyses to parous females (in the supplementary material [Stable 35] we also report the analyses with the increased data set including nulliparous females). We tested for 2nd order interactions between both study site and age of the dependent offspring and all other fixed effects to evaluate if patterns may differ among study sites or with female reproductive state. Only male- (parous) female associations with known start and end times were incorporated in the analyses (N=960) (the results remain the same if we also include associations without a known start or end time). To avoid a bias against long male-female associations, we included associations 1) that were known to last up to the end of the focal follow day or 2) where the partner was already in association when the focal follow was started. Copulations are rarely observed, but because they last several minutes (Fox, 1998; Knott et al., 2010) and involve two individuals in close proximity, which is rare in orang-utans, we can be confident that no copulations were missed by observers during focal follows. Because short interactions, like failed female-resisted attempts, may have been missed, we restricted the analyses to copulations (the results remain the same if we also include known failed attempts, see suppl. mat. Stable 33). The data are not zero-inflated, and we report the ordinary, binomial GLMMs here, rather than 0-inflated models. Nevertheless, all the analyses were also conducted using the package 'glmmTMB' (Brooks et al., 2017) accounting for potential 0-inflation (the results are reported in the suppl. mat. Stable 34), and the results of the two approaches revealed similar patterns. The identity of both female and male were added as crossed random intercepts to all analyses on the occurrence of copulations during dyadic associations.

Context and consequences of female resistance

We investigated the context and consequences of female resistance behaviour (compared to no resistance) based on separate instances of sexual interactions, including both attempts and copulations. Limited sample size forced us to include all females (parous and nulliparous) in the analyses. Based on the visual inspection, the residual distribution was closer to normal including the full data set and the analyses had fewer singularity issues. Female parity was included as a fixed effect in all analyses, and possible 2nd order interactions with other fixed effects were tested. The analyses including only parous females are reported in the supplementary materials (Stable 39-41). In all the models described below, the study site, male morph and zFAI were included as fixed effects. Both male and female identity were included as crossed random intercepts to account for individuals represented several times in the data set, whenever possible and not indicated otherwise.

Presence of other males

Because the analyses on the copulation probability during dyadic associations did not allow inferences about when the male was displaced relative to the timing of the copulation, we investigated the relationship between female resistance and the immediate presence of other individuals (N=422 sexual interactions). We set up a binomial generalized linear mixed effects model to check if females were more likely to resist male-initiated sexual interactions if additional males, unflanged and flanged males separately, or other individuals were present.

Arrival of new males

We also assessed the probability of other males arriving shortly after sexual interactions (within the next hour). For this, we only considered sexual interactions which occurred on days when females were the focal individual and followed until the night nest. A binomial generalized linear model was set up to evaluate if a new male arrived within 1 hour after a sexual interaction occurred. Because of the missing variation in our relatively small data set, we could not include male and female identity as crossed random intercepts. Therefore, we took only the last copulation of an association dyad into account to minimize pseudo-replication (N=187 sexual interactions).

To evaluate the actual latency (min) to the arrival of a new male on the same day after sexual interactions, a linear mixed effects model was formulated. The latency (min) to the arrival of another male was square-root-transformed to normalize the residual distribution. Only the last copulation of a particular dyad imminently preceding the arrival of a new male was considered (N=108 sexual interactions with a new male arriving later on the same day) (e.g. if there were several copulations in a particular dyad, only the latency from the copulation immediately preceding another males' arrival was taken into account). Both female and male identity were added as crossed random intercepts to account for repeatedly having the same individuals in the analyses.

Association maintenance

To evaluate if associations ended sooner after copulations with female resistance, we ran a Cox proportional hazard mixed-effect model using the 'coxme' package (Therneau, 2018). Only the latency to the end of the association after the last observed sexual interaction in a particular dyad was included (N=258 last sexual interactions of which 162 dyadic associations with a known end). We used right-censored data to account for the dyadic associations of which the end was unknown, because the focal follows were ended prior to the end of the association. The latency (hours) to the end of the association was calculated from the end of the last sexual interaction to the end of the association. Both male and female identity were included as crossed random intercepts in the survival analysis. To illustrate the Kaplan-Meier survival curves, we used the packages 'survival' (Therneau, 2015) and 'survminer' (Kassambara and Kosinki, 2018).

Results

Occurrence of copulations in dyadic associations

Consistent with previous findings, the probability of both resisted and non-resisted copulations during dyadic associations increased with increasing age of the dependent offspring of parous females and was higher for unflanged than flanged males, but was not related to local zFAI (Table 13). The models improved significantly, when we added association duration, dyadic familiarity and measures of male-male competition (*non-resisted:* $\chi^2_{7,12}$=39.88, P<0.0001; *resisted:* $\chi^2_{7,12}$=30.37, P<0.0001). Both non-resisted and resisted copulations became more likely as dyadic association duration increased (*non-resisted:* β=0.841±0.181, OR=2.32, z=4.647, P<0.001; *resisted:* β=0.726±0.192, OR=2.07, z=3.783, P<0.001). However, dyadic familiarity did not predict the occurrence of copulations (*resisted:* β=0.004±0.183, OR=1.00, z=0.022, P=0.98; *non-resisted:* β=0.031±0.144, OR=1.03, z=0.218, P=0.83).

Table 13 Probability of resisted and non-resisted copulations*:* Binomial GLMM for the occurrence of copulations (no/yes) in a given dyadic male-female association depending on study site, age of the dependent infant (y), male morph (unflanged vs. flanged), Fruit Availability Index, association duration, the overall time a dyad was ever seen together, the number of males in association on this particular day, and if the male in association was displacing another male or was displaced by another male (N=960 male-female associations with known start and end from 31 parous female and 174 male IDs). The model comparisons using likelihood ratio tests are reported below each full model (*Note:* z = the continuous, fixed factors were z-transformed in order to facilitate model convergence; I=Intercept; C=control factor; F=fixed factor)

Response	Fixed effects		Estimate	SE	Odd's ratio	z value	P value
Resisted copulations	Intercept	I	-4.112	0.664			
	Site (Suaq vs. Tuanan)	C	-0.140	0.617	0.87	-0.227	0.820
	z Age of dependent infant (y)	**C**	1.623	0.360	5.07	**4.512**	**<0.001**
	Male morph (unflanged vs. flanged)	**C**	-1.898	0.516	0.15	**-3.676**	**<0.001**
	z Fruit Availability Index	C	0.077	0.192	1.08	0.402	0.688
	z Association duration (h)	**F**	0.726	0.192	2.07	**3.783**	**<0.001**
	z Dyad time (h)	F	0.004	0.183	1.00	0.022	0.982
	Number of other males in association	F	-0.130	0.194	0.88	-0.666	0.505
	Displacement by another male	**F**	1.047	0.417	2.85	**2.511**	**0.012**
	Displacing another male	F	0.433	0.469	1.54	0.923	0.356
	Comparison to null model: $\chi^2_{3,12}$ =95.34, P<0.00001, ΔAIC=77.34, pseudo-R^2=0.22						
	Comparison to control model: $\chi^2_{7,12}$=30.37, P<0.00001, ΔAIC =20.36						
Non-resisted copulations	Intercept	I	-3.947	0.463			
	Site (Suaq vs. Tuanan)	C	0.347	0.482	1.41	0.720	0.471
	z Age of dependent infant (y)	**C**	1.357	0.308	3.88	**4.405**	**<0.001**
	Male morph (unflanged vs. flanged)	**C**	-1.659	0.480	0.19	**-3.460**	**0.001**
	z Fruit Availability Index	C	0.233	0.173	1.26	1.347	0.178
	z Association duration (h)	**F**	0.841	0.181	2.32	**4.647**	**<0.001**
	z Dyad time (h)	F	0.031	0.144	1.03	0.218	0.828
	Number of other males in association	F	-0.294	0.212	0.75	-1.388	0.165
	Displacement by another male	**F**	-0.271	0.475	0.76	-0.570	0.568
	Displacing another male	F	1.124	0.443	3.08	**2.534**	**0.011**
	Comparison to null model: $\chi^2_{3,12}$=96.93, P<0.00001, ΔAIC =78.93, pseudo-R^2=0.13						
	Comparison to control model: $\chi^2_{7,12}$=39.88, P<0.00001, ΔAIC =29.88						

Female resistance was not predicted by the (known) number of males that were in association on the same association days as the male-female dyad (*resisted:* β=-0.130±0.194, OR=0.88, z=-0.666, P=0.51; *non-resisted:* β=-0.294±0.212, OR=0.75, z=-1.388, P=0.17), but it was by the occurrence of displacement events (Figure 18). Resisted copulations were more likely when the male was displaced

by another male at any time during the current dyadic association (*resisted:* $\beta_{displaced}$=1.047±0.417, OR=2.85, z=2.511, P=0.01), but not when he had himself displaced another male (*resisted:* $\beta_{displacing}$=0.433±0.469, OR=1.54, z=0.923, P=0.36) (Figure 18). In contrast, non-resisted copulations were more likely when the male was displacing another male (*non-resisted:* $\beta_{displacing}$=1.124±0.443, OR=3.08, z=2.534, P=0.01), but not when he was displaced by another male (*non-resisted:* $\beta_{displaced}$= -0.271±0.475, OR=0.76, z=-0.570, P=0.57) (Figure 18). Various second-order interaction terms including study site or the age of the dependent offspring and any other fixed factor did not lead to an improved fit of the model and thus, did not appear to explain more variation.

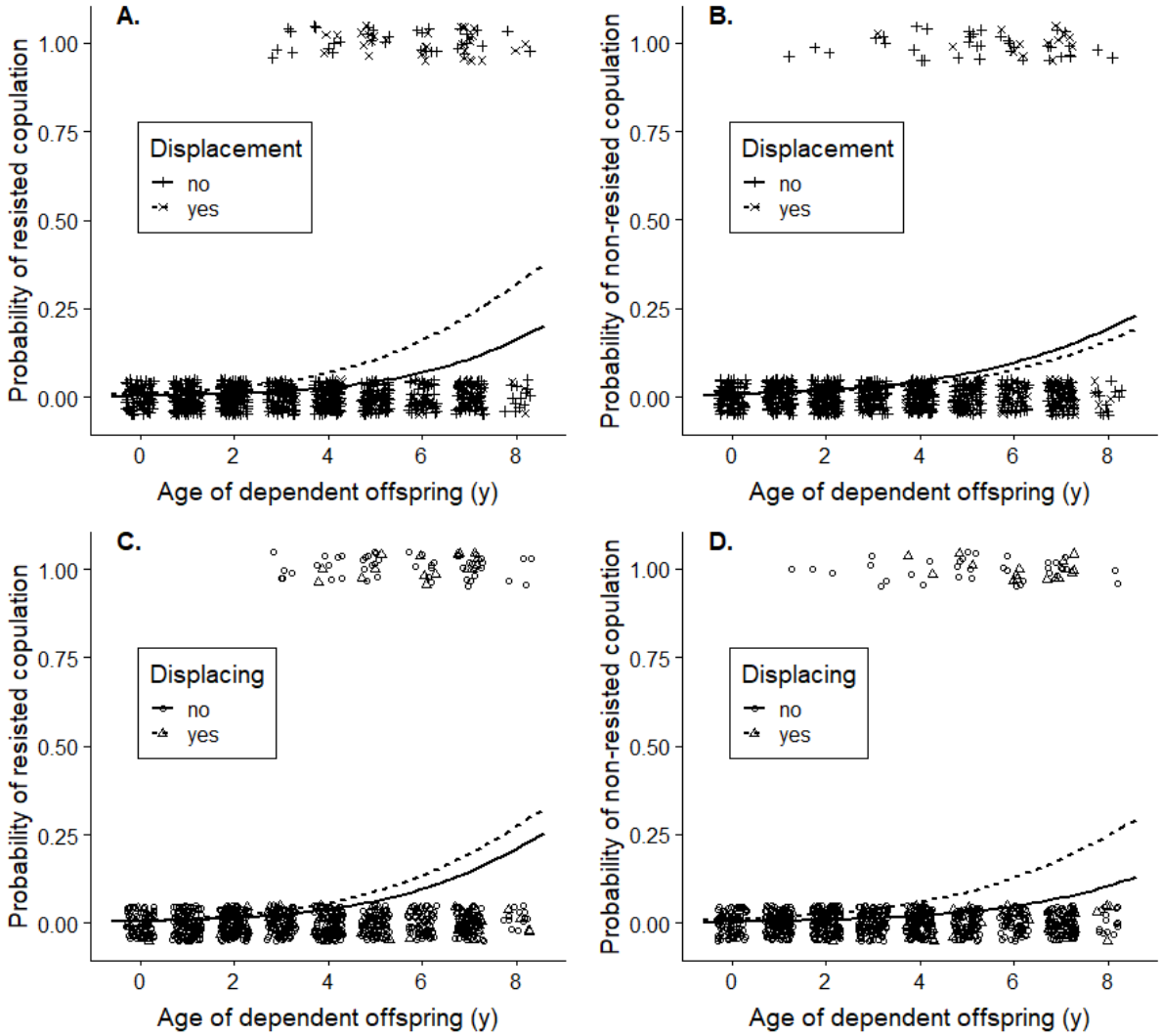

Figure 18 Occurrence of resisted (A, C) and non-resisted (B, D) copulations depending on the age of the dependent offspring of parous females (*x-axis*) and if the male partner was displaced (*top: A, B*) or had displaced another male (*bottom: C, D*). Data points are based on separate dyadic associations (N=960). A jitter function was applied to the raw data points to make them more visible. The solid line indicates the model predictions, when there was no displacement/displacing male and the dashed line indicates the model predictions when displacement/displacing event occurred.

Occurrence and context of coercive handholding

The few direct observations of coercive mate guarding (N=15) concerned both flanged and unflanged males at Tuanan (6 different individuals; 3 flanged and 4 unflanged males; one male as both unflanged and flanged male). Unflanged males were observed to coerce nulliparous and parous females, while flanged males only actively mate guarded parous females (Figure 19C). Hand-holding could last

for hours (van Schaik et al., 2006). Especially relevant here is that coercive hand-holding was more often observed on days when there were multiple males in association (N=13) than when the coercing male was the only (known) male in association on the day of occurrence (N=2) (Figure 19A). No clear pattern is apparent with respect to the mate guarding male's dominance relationship with other males present, as observed on the day of the coercive handholding event (Figure 19B). Intriguingly, an unflanged male was observed to put his hand onto the mouth of a female presumably to hinder her from vocalizing. The female repeatedly emitted "kiss-squeaks" before he covered her mouth.

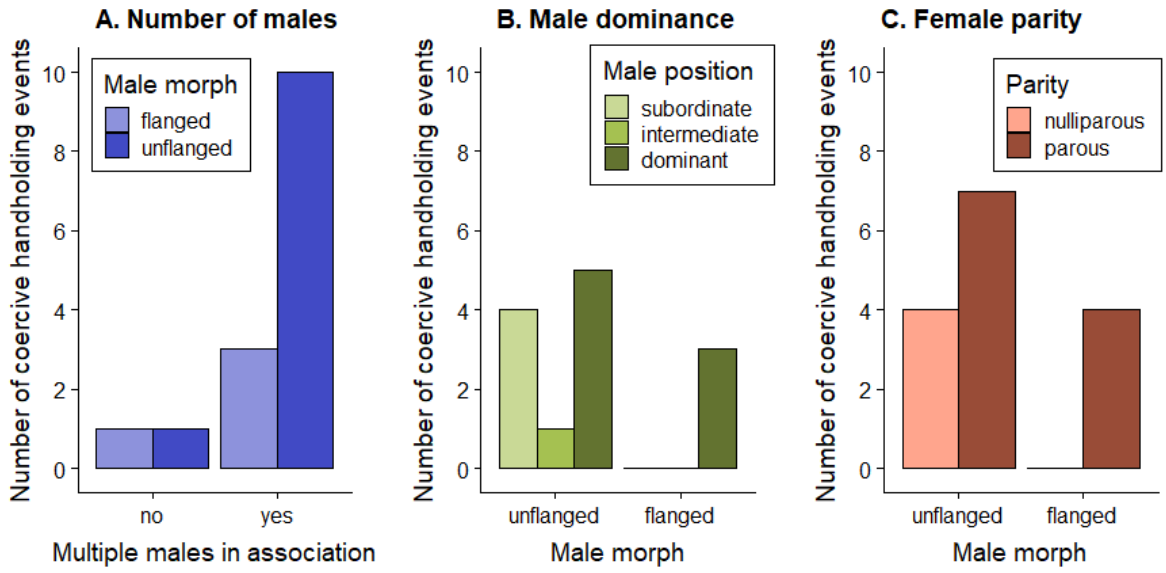

Figure 19 Counts of all occurrences of coercive handholding by males at Tuanan, Kalimantan (N=15), throughout the entire study period of 15 years depending on A. if there were additional males in association and male morph, B. given that there were multiple males (N=13), the dominance relationship among the males present that day (i.e. who maintained closest proximity to and remained in association with the female) and male morph, C. Female parity and male morph.

Context of female resistance

Presence of other males during sexual interactions

The majority of the sexual interactions occurred when no additional male was within 50m of the dyad (73% [307 of 422 interactions]). Yet, if there was also a flanged male in association, females were more likely to resist during sexual interactions (71 % of sexual interactions with unflanged males when a flanged male was around [22/31]; β=1.450±0.671, OR=4.26, z=2.161, P=0.03) (Table 14; Figure 20A). Accordingly, adding the presence of flanged males improved the model fit significantly compared to the model containing only site, female parity, male partner morph and zFAI ($\chi^2_{7,8}$=5.27, P=0.02). However, the presence of an additional unflanged male did not increase the probability of female resistance during sexual interactions (55 % of sexual interactions with female resistance when an additional unflanged male (and no flanged male) was within 50m [46/84]; β=0.114±0.384, OR=1.12, z=0.297, P=0.77). Also the presence of any other individual (excluding the female's dependent offspring, who is always present) did not relate to the probability of female resistance (β=0.088±0.409, OR=1.09, z=0.215, P=0.83). The full tested model was significantly better than the null model ($\chi^2_{7,8}$=5.27, P=0.02). Adding interactions between sites or female parity and the presence of other individuals (unflanged and flanged males and others) did not further improve the full model fit. Interestingly, for the analysis including parous females only, a female's resistance was predicted only by the interaction partner's morph and the presence of an additional flanged male and not by her reproductive state (age of the dependent offspring) (suppl. mat. Stable 39).

Table 14 Probability of female resistance behaviour: Binomial GLMM output on the probability of female resistance behaviour in a given dyadic sexual interaction depending on site, female parity, the interaction partner morph, the presence of additional flanged and unflanged males and any other (non-adult male) association partner and zFAI ($\chi^2_{3,10}$= 30.31, P<0.0001, ΔAIC=18.27, N=422 sexual interactions of 34 female IDs and 87 male IDs)

	Estimate	SE	Odd's ratio	z value	P value
Intercept	-0.617	0.813			
Site (Suaq vs. Tuanan)	-0.394	0.835	0.67	-0.472	0.637
Flanged male present (no vs. yes)	1.450	0.671	4.26	**2.161**	**0.031**
Unflanged male present (no vs. yes)	0.114	0.384	1.12	0.297	0.767
Other individual present (no vs. yes)	0.088	0.409	1.09	0.215	0.830
Parity (nulliparous vs. parous)	1.628	0.572	5.09	**2.847**	**0.004**
Partner morph (unflanged vs. flanged)	-1.929	0.558	0.14	**-3.459**	**0.001**
zFAI	0.228	0.169	1.26	1.348	0.178

Latency to the arrival of new male associates

The probability of a new male arriving within 1 hour after a sexual interaction was higher when a female resisted (0.20±SE 0.04 of resisted interactions) than if she did not (0.05±SE 0.02 of non-resisted interactions) (β=1.528±0.636, OR=4.61, z=2.401, P=0.02) (Figure 20B), and the full model was significantly better than the null model (χ^2_5 = 15.77, P=0.008; suppl. mat. Stable 36). Also, the absolute latency (min) to the arrival of the new male associate, given that a male arrived after a sexual interaction, was significantly shorter when the female resisted (mean 93±SE 16 min [median=54min]) than when there was no female resistance (mean 184±SE 20 min [median=140min]) (β=-3.768±1.447, t= -2.604, P=0.01, suppl. mat. Stable 37). Even though this pattern seemed more pronounced at Tuanan than at Suaq (Figure 20C), adding the interaction between site and female resistance only marginally improved the model's fit ($\chi^2_{9,10}$ =3.20, P=0.07). The probability of new male arrivals and the latency to a new arrival if one arrived after sexual interactions were not predicted by female parity, the arriving male's morph, or fruit availability (suppl. mat. Stable 36, Stable 37).

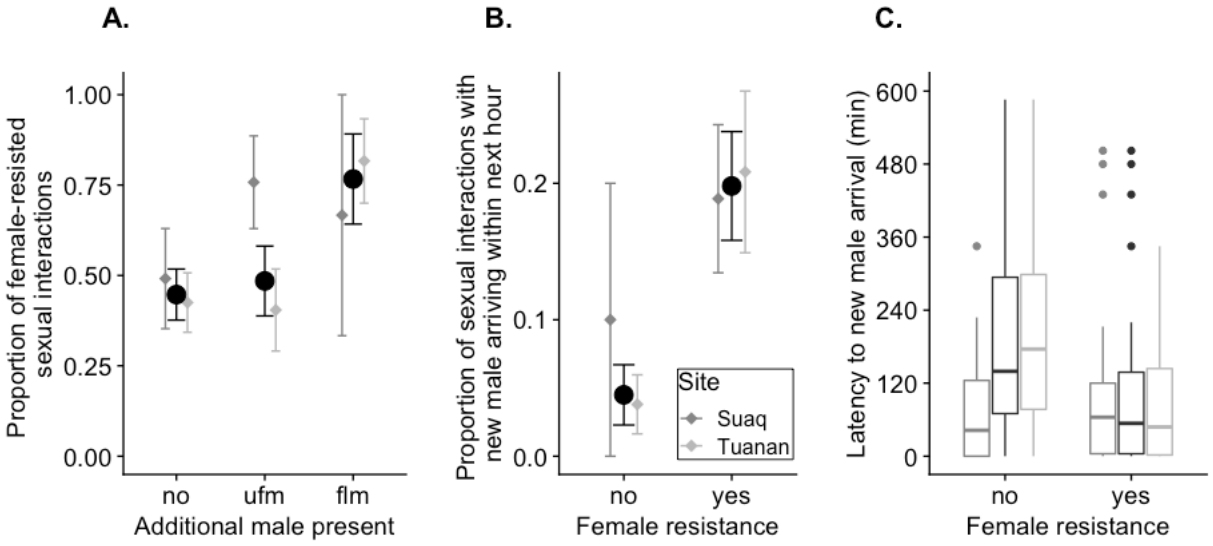

Figure 20 Context of sexual interactions and female resistance: A. Proportion of female resistance to male-initiated sexual interactions (*y-axis*) depending on the presence and morph of additional males (no= no other male; ufm= unflanged male; flm= flanged male) by study site (*dark grey:* Suaq, *light grey:* Tuanan). The data points illustrate the mean and standard error based on individual female mean resisted sexual interactions in each condition (in black over all females and both populations). B. Proportion of sexual interactions with the arrival of a new male (< 50m of the dyad) in the subsequent hour depending on the absence ("no") /presence ("yes) of female resistance (*x-axis*). The data points (with standard errors) illustrate the overall mean proportion of sexual interactions with a new male arriving within the next hour (*black:* overall; *dark grey:* Suaq; *light grey:* Tuanan). C. Latency to the arrival of a new male associate after a sexual interaction (min) depending on female resistance (*x-axis*) and by study site (legend see 20B.). The boxplot shows the median latency to a new male arrival (<50m of the male-female dyad), given that there was a new male associate on the same day, based on separate sexual interactions.

Latency to the end of an association

Most dyadic associations ended the same day after the last copulation (71%; 115 of 162 associations with a copulation and known end time). If there was female resistance during the last copulation, the median latency to the end of association was 2 hours (mean=10.6 ±SE 2.4 h), while the median was 5 hours without female resistance (mean= 14.3±SE 2.3 h), given that the end time of the association was known. The survival analysis correspondingly revealed that female resistance led to a faster end of the association, when controlling for site, local fruit availability, female parity and partner morph (suppl. mat. Stable 38). Although the full Cox proportional hazard mixed model was not significantly better than the null model (χ^2_5= 8.76, P=0.12), the reduced model including female resistance behaviour only was (χ^2_1=5.06, P=0.02) and accordingly the female resistance behaviour predicted a faster end of the association (β=0.419±0.173, HR= 2.52, z=2.430, P=0.02) (Figure 21).

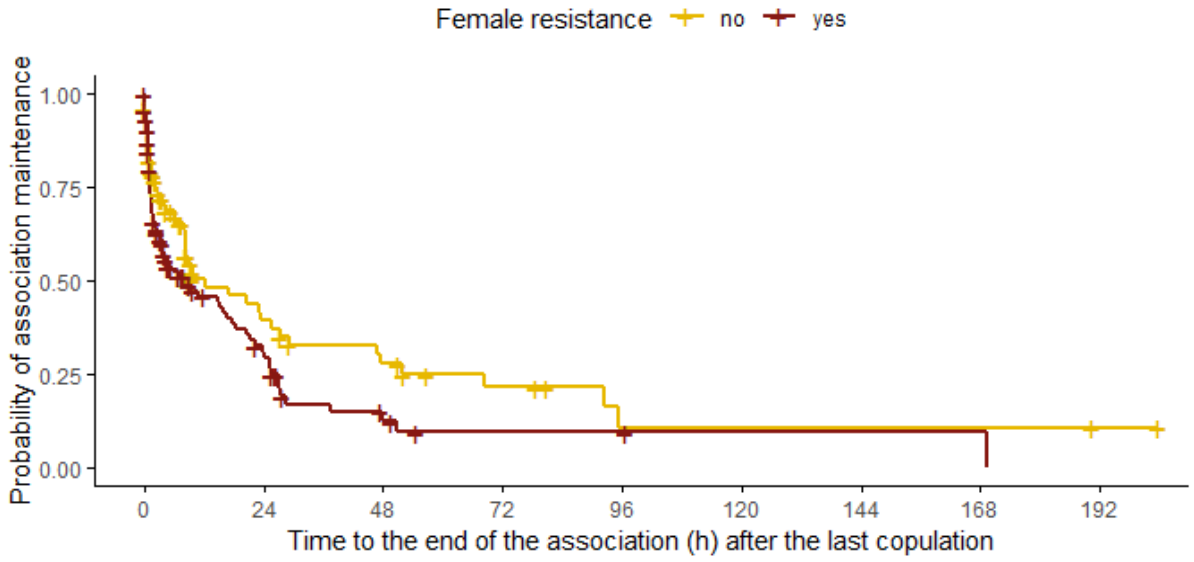

Figure 21 Survival curve for the maintenance of a dyadic association after the last observed sexual interaction depending on the female behaviour during the sexual interaction (*yellow*= non-resisted; *red*= resisted). *Note:* The figure shows the direct relationship between female resistance and association maintenance and is not corrected for the other variables, i.e. male and female identity, study site, female parity, partner male morph and FAI, which were included in the survival analysis.

Discussion

Sexual coercion has long been regarded as a male mating strategy in orang-utans. Our results suggest both the males' decision to coerce and the females' decision to resist are highly context-dependent. On the one hand, males force copulations when at risk of displacement and hence follow a "*now-or-never*" tactic. This is further underlined by the coercive mate guarding at the population of Tuanan, which is most likely to occur on days with other males in vicinity, and thus, when males are at risk of losing access to a female. On the other hand, females appear to follow a *"not-you-now"* tactic, as they resist mating with subordinate males especially if more dominant males are in vicinity. Females were less likely to resist mating initiations with dominant males who displaced other males. As interaction terms were not significant, there was no evidence for changes in these mechanisms with the females' reproductive status. One caveat is that we found these results with a crude measure of female reproductive state: the age of the dependent offspring. Although orang-utan males probably do not have better information about the proximity to ovulation (Fox, 1998; Knott et al., 2010; Nadler, 1981), future studies should try to account for the actual female ovulatory state.

The probability of male mating initiation or female resistance did not depend on dyadic familiarity, which further emphasizes the context-dependence of the sexual conflict over mating in

orang-utans. Nonetheless, long-term male-female relationships cannot be ruled out altogether (Mitra Setia et al., 2009; Utami Atmoko et al., 2009a) and future studies are needed to show if increased dyadic association frequency is reflected in an increased male siring success, as reported from other fission-fusion systems (chimpanzees: Langergraber et al., 2013). Frequent associations with specific females are opportunities for males to obtain more accurate information on her reproductive status, especially for subordinate males who cannot rely on female choice.

The probability of copulation with or without female resistance increased with the duration of the association. Male-female associations, especially when long, tend to be male-maintained (chapter 3), and thereby can be taken as evidence for male mating effort. Because ovulation is concealed from males, and females only advertise fertility behaviourally, if at all (Fox, 1998; Knott et al., 2010), non-preferred males likely use repeated associations with females to monitor the female's sexual activities. Although the low copulation rates suggest that even males are selective (Schürmann and van Hooff, 1986; Utami Atmoko et al., 2009a), males were previously reported to mate with females which are highly unlikely to conceive (Knott et al., 2010). With the link to male-male competition uncovered here, these likely non-conceptive copulations are explained to some extent: If males invest in maintaining long associations with females and are displaced, they are triggered to copulate, or alternatively, if they are displaced, they may remain in the vicinity and attempt sneak copulations. Indeed, the link between copulations and the presence of other more dominant males nearby suggests that subordinate males take the presence of other males as a proxy for female reproductive state. Thus, the size of a female's offspring may not be the only rule of thumb that males follow to estimate a female's reproductive status (Fox, 1998), but they may "eavesdrop" on both other males' sexual interest and the females' own behaviour towards other males. This is evident by unflanged males often following consorting dyads in Sumatran populations (Schürmann, 1982; Utami Atmoko et al., 2009a), as they may wait for sneak copulation opportunities (Fox, 2002).

Neither male mating initiation, nor female resistance probability or its consequences differed between the two study sites of Suaq and Tuanan and thus, presumably, species (*P. abelii, P. pygmaeus*). We could also not find any evidence that mechanisms differed between the two sites (i.e. interaction terms), apart from the trend of a quicker arrival of males after female-resisted copulations at Tuanan. At both study sites, female resistance was predicted by displacement events and the presence of more dominant males nearby. Previous studies reported variation in the overall coercion rates of both unflanged and flanged males connected to the varying extent of male developmental arrest and variation in the male dominance relationship stability (Delgado and van Schaik, 2000; Dunkel et al., 2013; Pradhan et al., 2012). Our results do not contradict such differences between populations: depending on both the sociability and the male dominance relationship stability of a population, displacement frequency of specific individuals and male morphs may vary and thereby lead to these observed population differences (for a detailed discussion see suppl. mat.). While in less sociable populations displacement events are more likely to lead to the end of an association, because of the high costs of association and the reduced social tolerance (van Schaik, 1999), in more sociable populations displaced males may be more likely to remain in the vicinity of a consorting dyad and subsequently attempt to sneak copulations.

Resistance may give females leverage over males (sensu Lewis, 2018), as it eventually leads to a quicker arrival of additional males and to a faster end of an association with harassing males. However, the mechanism and particularly the directionality of the observed link between male competition and female resistance needs further investigation. We cannot conclusively resolve whether the displacing or arriving male was the immediate trigger for the male mating initiation and female resistance, or instead the female resistance itself attracted additional males (female resistance is often accompanied by loud vocalizations of the female [suppl. mat. Sfigure 21] and her dependent offspring, and other noise such as crashing branches). However, the two mechanisms are not exclusive, and even if the first one holds,

nearby males were more likely and faster to move to the mating dyad's location, suggesting that females incited male-male competition with their resistance. Male attempts to reduce detectability by other males during associations with females provide further support for the second scenario: loud female protest vocalizations in the food transfer context were previously reported to lead to a faster end of male-female association (van Noordwijk and van Schaik, 2009). In the current study we present anecdotal evidence for a male trying to hinder a female from vocalising by putting his hand on her mouth. Likewise, flanged males themselves reduce their long calling frequency when in association with females (Mitra Setia et al. 2009; Mitra Setia and van Schaik 2007; but not in all populations: Askew and Morrogh-Bernard 2016), presumably to avoid attracting potential male mating competitors. Playback experiments with female vocalizations could help to understand the males' reaction to female protest vocalizations. Also the female reaction to signs that other males are nearby need further investigation. Sexually active females reportedly approach long calling males (Fox, 2002; Mitra Setia and van Schaik, 2007; Spillmann et al., 2010). Detailed analysis of female ranging responses to long calls when either alone or in association with another male are needed to investigate if females actively lead one male to another and thereby incite male competition, and/or seek for protection from harassing males (Mesnick, 1997).

The likelihood of female resistance increased with the presence of an additional flanged male, but not with the presence of unflanged males or other individuals. Bystander effects on female sexual initiations have been found in chacma baboons (Baniel et al., 2019) and macaques (long-tailed macaques: Overduin-de Vries et al., 2013; rhesus macaques: Overduin-de Vries et al., 2012). Whereas chacma baboon and macaque males, to some extent, were also less likely to initiate mating with additional (higher-ranking) males in vicinity (ibid.), orang-utan males initiated copulations despite the presence of dominant males. In more social (group-living) species sanctions for sneaky mating may be high for both males and females: Punishment of the female (Baniel et al., 2019; sensu Clutton-Brock and Parker, 1995) and direct male aggression towards sneaky mating males (Overduin-de Vries et al., 2012). In contrast, due to the dispersed mating system, orang-utan males were rarely reported to intervene in copulations (Fox, 2002). Therefore, there are no reports of dominant males punishing either copulating subordinates or promiscuously mating females by physical aggression. Moreover, male aggression towards females, outside the context of copulations, is extremely rare (chapter 3), indicating that delayed punishment or intimidation is absent too.

From an ultimate perspective, female resistance behaviour appears congruent with an infanticide avoidance mating strategy. In the absence of more dominant males, females tolerate copulations with subordinate males for paternity dilution purposes. Yet, if a more dominant male is in the vicinity, females may resist mating with the current male, and thus i) obtain protection (Mesnick, 1997) and end an involuntary association (van Noordwijk and van Schaik, 2009) and ii) signal their non-willingness to mate with a subordinate male to the dominant male, and thereby increase the dominant male's assessment of his paternity chances and the actual chances as well (van Schaik et al., 2004). It remains to be tested if female resistance and vocalizations even function to attract more dominant males. Note, however, that such strategic use does not imply strategic intentions on the part of the female. At the mechanistic level, females appear to be highly distressed. Thus, female-resisted copulations still qualify as sexual coercion, as males constrain female mate choice (Smuts and Smuts, 1993), and male-female mating interests are at odds (Arnqvist and Rowe, 2005; Parker, 1979). Yet, the occurrence of sexual conflict over mating in orang-utans can only be understood when taking the immediate context into account and the need for female counterstrategies to infanticide in a dispersed mating system. Although direct evidence for the occurrence of infanticide remains elusive in wild orang-utans (Knott et al., 2019), female orang-utans certainly meet the criteria to be vulnerable to infanticide with their high lactation to gestation ratio (gestation of 245 days: Graham, 1988; lactational infertility of ~ 6 years van Noordwijk et al., 2018) and their solitary lifestyle (Rijksen, 1978; van Schaik, 1999), i.e. the absence of permanent associations, which could provide protection against infanticidal attacks (van Schaik and Kappeler,

1997). In addition to our current results, there is increasing evidence for efficient female counterstrategies to infanticide in orang-utans including extended female mating periods (chapter 4), female choice depending on their ovulatory state and male quality (Fox, 1998; Knott et al., 2010) and male dominance relationship stability (Utami Atmoko and Setia, 1995), and mother-infant behaviour around males (Scott et al., 2019). In conclusion, female-resisted copulations in orang-utans are highly context-dependent and in agreement with a female infanticide avoidance strategy.

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Chapter 6: General Discussion – Sexual Conflict in Orang-utans

The orang-utan pattern

The occurrence of forced copulations in orang-utans can only be understood in the light of socio-ecological factors, female counterstrategies to infanticide and the immediate social context leading to conflicting male and female mating interests. With this thesis, we shed a little light onto the complexity of orang-utan intersexual dynamics and provided a basis for comparative studies between different genera to further our understanding of the evolution of sexual coercion and sexual conflict in primates in general.

Evaluation of hypotheses for forced copulations in orang-utans

We presented five different, non-mutually exclusive hypotheses to explain colliding mating interests in orang-utans at the beginning of this thesis (p. 33; Table 2). The aim of this discussion is to sort the evidence for and against them, and evaluate especially the *Infanticide Avoidance Hypothesis*. Three of the hypotheses can be rejected with the information currently available.

First, the *Male Quality Hypothesis* alone does not explain the occurrence of sexual coercion in orang-utans. Both unflanged and flanged males were observed to coerce, as suggested by previous studies (Knott, 2009; Mitani, 1985a; Utami Atmoko et al., 2009a), and most importantly individual males had both forced and unforced copulations (chapter 2). Yet, as suggested by previous studies (Galdikas, 1985b; Utami Atmoko and van Hooff, 2004), we found evidence for alternative reproductive strategies of the two male morphs: Unflanged males exhibit higher association, copulation and coercion rates, whereas flanged males, who are preferred by females, are more selective when to associate and copulate, and are rarely observed to force mating. These findings suggest that unflanged males may not only experience female resistance more frequently, because they are less preferred, but also because they copulate more frequently. All in all, forced copulations are neither a trait characterizing particular individual males nor a strategy specific to one male morph, unflanged males (chapter 2). Furthermore, we did not find any evidence for dyadic familiarity relating to either male coercive tendencies or female resistance (chapter 5), i.e. particular males discriminated against by particular females. Males that forced copulations had quite often mated with the same female on other occasions without being resisted. Hence, even if there was variation between females in their preferences, it is not reflected in their resistance behaviour.

Second, the *By-product of Reproductive Physiology Hypothesis*, which predicts that male and female mating interests collide during periods when females are not fertile, appears unlikely. The likelihood of resistance by parous females did not decrease as conception approached. Even though we did not have accurate measures of the female reproductive state (i.e. reproductive hormone measures),

previous studies found female resistance also around ovulation (Knott et al., 2010). However, the predictions of the *By-product* hypothesis may hold for nulliparous females, whose resistance rates decreased with approaching conception (chapter 4). Such a pattern is likely associated with nulliparous females' learning process of how to behave around males (O'Connell et al., 2019). Third, the *Artefact of Habituation Status Hypothesis* was not explicitly tested in this thesis, but we observe forced copulations in male-female dyads where both male and female are well habituated and in captivity (Nadler, 1981). This is why we could reject this hypothesis already in the introduction. Nevertheless, with the link we found to male-male competition (chapter 5), we cannot exclude that male coercion is also triggered by other (social) stressors, which still need to be examined. In any case, the existence of forced copulations in general, however, cannot be ascribed to the habituation status of individuals *per se*.

This leaves two explanations for the occurrence of mating conflict in orang-utans, and with this thesis we found support for both of them: the *Infanticide Avoidance Hypothesis* and the *Price for Not Signalling Fertility*. To begin with the last idea, females experience elevated scramble competition during male-maintained associations, in the form of reduced feeding and increased moving time. Moreover, female cortisol levels increased with an increasing number of consecutive days in association with males, whereas we found no significant increases on days with forced copulations (chapter 3). Males may benefit from associations with females both directly as it provides them with an opportunity to mate, and indirectly because it enables them to monitor the females' reproductive status and sexual activity. Yet, paradoxically, females do not reliably advertise fertility which would presumably lead to increased association and mating frequency during the advertised periods, but no such attention at other times (sensu Wrangham, 2002). The absence of fertility advertisement, however, makes females vulnerable to sexual coercion during an extended period (Figure 22), because ovulation appears to be concealed and males mate independently of the female reproductive state (Knott et al., 2010; Nadler, 1981; chapter 4). Female orang-utans may face a trade-off between the costs of association and the benefits of paternity confusion ('cost-of-sexual-attraction' hypothesis [Wrangham, 2002]). The *Price for Not Signalling Fertility Hypothesis*, therefore, only makes sense under the assumption of the need for paternity confusion. Otherwise, female orang-utans would be expected to signal fertility reliably during the short periovulatory window. Thus, forced copulations may be the price females pay for not advertising fertility and having concealed ovulation. Interestingly, female orang-utans do advertise pregnancy with small, but clearly visible labial swellings (Galdikas, 1981; Schultz, 1938). Future studies need to evaluate, if such advertisements of non-availability lead to lower association and coercion frequencies, and thus, function as a counterstrategy to sexual coercion. Our unpublished data suggests that sexual interactions with pregnant females who exhibit a labial swelling are indeed extremely rare (1 out of 30 pregnancy copulations with a female who exhibited a labial swelling, including failed attempts 3 out of 35). In sum, orang-utan females are likely constrained by the costs of association in their sexually active periods and thus, do not exhibit fertility advertisements during an extended period, while needing to confuse paternity (Figure 22).

This leads us to the *Infanticide Avoidance Hypothesis*, which predicts that male and female mating strategies are at odds about the optimal paternity distribution (van Schaik et al., 2004). Specifically, females are expected to follow a mating strategy as to distribute paternity perception among different males, while concentrating the highest paternity probability in dominant males who would pose the highest risk of infanticide if they do not perceive a high paternity certainty. Throughout this thesis we found evidence that orang-utan intersexual patterns are consistent with such female paternity confusion strategies (chapter 3, 4, 5) and propose therefore that sexual coercion in orang-utans is a consequence of the risk of infanticide (chapter 5). Before evaluating how our findings on sexual coercion are consistent with the predictions of the *Infanticide Avoidance Hypothesis*, we discuss how the concept of sexually selected infanticide appears to have shaped orang-utan mating patterns in general (Figure

22). Infanticide meets the criteria as sexually selected male strategy if i) killing the infant leads the female to a faster return to fertility, ii) the male is unlikely to kill his own progeny and iii) males greatly increase their chances of mating access after the death of the infant (van Schaik, 2000).

The risk of infanticide as selection pressure

Infanticide has never been directly observed in wild orang-utans (Beaudrot et al., 2009; Knott et al., 2019; but once in captivity: Mallinson, 1984) and infant mortality is extremely low (van Noordwijk et al., 2018). Even so, their life history – with the extremely high lactation to gestation ratio – qualifies orang-utan females (and their infants) as vulnerable to infanticide (van Schaik, 2000) (Figure 22). Theoretical approaches on the occurrence of sexual conflict arising from the risk of infanticide were based on group-living primates (e.g.: van Schaik et al., 2004) and sexually selected infanticide has mostly been reported in social and less in solitary species (review: Lukas and Huchard, 2014), with the exception of solitary carnivores (e.g. leopards: Balme and Hunter, 2013; bears: Bellemain et al., 2006). The dispersed mating system of orang-utans has led to the assumption that individual males cannot efficiently monopolize female sexuality over an extended period (point iii from above) and thereby, to reject infanticide as a sexually selected male strategy in orang-utans (Beaudrot et al., 2009). Increasing evidence for (efficient) female sexual and social counterstrategies to infanticide have accumulated, however (Fox, 2002; Knott et al., 2010; Mitra Setia and van Schaik, 2007; Scott et al., 2019; Utami Atmoko et al., 2002). The actual rate of infanticide by males is the result of a coevolutionary informational arms race between these female counterstrategies (distribute paternity assessments to reduce the infant's vulnerability) and the male's attempt to monopolize female sexuality (by obtaining accurate cues on female reproductive state) (Clarke et al., 2009) (Figure 23). Thus, even if a species qualifies as vulnerable to infanticide based on their life history, it may be absent because of efficient female counterstrategies (bonobos: Hohmann et al., 2019; reviews: Lukas and Huchard, 2014; Palombit, 2015). This arms race over paternity probabilities resulting from the risk of infanticide (sensu Clarke et al., 2009; van Schaik et al., 2004) has so far received little attention as relevant to explaining the occurrence of forced copulations in orang-utans (but see: Knott, 2009; Knott et al., 2010; and more generally Emery-Thompson et al., 2008; Stumpf et al., 2011, 2008).

Sexual counterstrategies to infanticide

Solitary females can less easily rely on effective social counterstrategies, like male or female allies, against infanticidal attacks (Palombit, 2000; van Schaik and Kappeler, 1997). Accordingly, orang-utan females reveal a variety of sexual counterstrategies to infanticide. First, females likely achieve polyandrous mating and thereby paternity confusion with their concealed ovulation leading to male-driven extended mating periods (for a detailed discussion chapter 4). The onset of mating was often years prior to conception, which indicates that 1) males do not have any information on the female ovulatory status (concealed ovulation), and 2) females may benefit from polyandrous mating by reducing the risk of infanticide. Male orang-utans range widely and are often absent from the study area for several months or even years (Utami Atmoko et al., 2009b). The concealed ovulation appears to lead to an ideal paternity assessment distribution: With the approaching conception, male competition around the female intensifies (Spillmann et al., 2017; e.g. fights: Utami Atmoko et al., 2009b) and females will eventually mate with the most dominant male, while subordinate males also achieve some mating access and perceive a non-zero chance of having sired offspring and refrain from killing the infant (especially if their future probability remains low too). Second, both female resistance and proceptivity in relation to her ovarian state and male identity has previously been shown to be consistent with an anti-infanticide mating strategy (Knott et al., 2010). Females can only express their pronounced positive and negative mate choice because they exhibit concealed ovulation, which allows them to evade male monopolization.

Third, female resistance changes with the immediate social context of mating interactions and is consistent with a strategy of distributing paternity chances among different males while ensuring a high probability for the most dominant male (chapter 5). Particularly, females were more likely to resist copulations by males who were displaced by other males in the course of the association, but not by males who had displaced another male. Thus, females resisted to mating initiations by males in the vicinity of more dominant males. Both the latency to the end of the association and to the arrival of a new male associate were shorter when females resisted (chapter 5). These results suggest that females may even directly incite male-male competition. Female choice would, thus, be the result of a comparative assessment of male strength, which in turn may lead to the optimal paternity distribution for females to reduce the risk of infanticide (sensu van Schaik et al., 2004). Anecdotal data suggests that in Bornean populations sexually active females approach long calls, when already in association with males (B. Spillmann, pers. comm.), whereas consorting Sumatran males approach long calls in what appears to be a slow chase (CvS, pers. comm). In Sumatra, there is also evidence for females inciting fights between rivals for local dominance and favouring consorting with the new dominant (Utami Atmoko and Setia, 1995). Whether females indeed actively incite male-male competition needs thorough testing in future studies, including the assessment of long call responses and simultaneous ranging patterns of males and females (detailed discussion in chapter 5).

This thesis is based on the evidence that females effectively conceal ovulation from males. A considerable drawback of our study is that we were not able to incorporate an accurate measure of female ovulatory state, but instead had to rely on either the time lag to conception or the age of the dependent offspring. The preliminary data on female progesterone metabolite levels suggests that ovulatory cycles are rare in the wild, and that male mating interest is likely independent of the female ovulatory state (see the suppl. mat. chapter 4). This is in accordance with female reproductive hormone levels being tightly linked to ecological factors (Knott et al., 2009) and previous findings on mating interactions with females known to be non-periovulatory (Knott et al., 2010; Nadler, 1981). Reaching a respectable sample size is difficult when it comes to linking reproductive hormone data with behavioural data for orang-utans (e.g. see chapter 3). However, eventually it would be desirable to i) link our progesterone data to oestrogen levels derived from urine samples, ii) obtain an extended period of repeated sampling record over several weeks from the same female (although so far we have avoided such sampling to avoid stressing females), and, iii) relate sexual investigations by males and subsequent mating with the ovulatory state and the level of volatile fatty acids to assess if males perceive olfactory cues (review: Drea, 2015; e.g. found in chimpanzees: Matsumoto-Oda et al., 2003). Finally, hair samples may be another possibility to acquire basic patterns on the overall temporal variation of reproductive hormones (Carlitz et al., 2014). In sum, a better understanding of the orang-utan female reproductive physiology is crucial to corroborate our conclusion and to confirm the concealed ovulation in orang-utans.

Social counterstrategies to infanticide

Even social counterstrategies to infanticide have been reported in (West) Sumatran populations. Lactating females remain in ear-shot associations with the dominant flanged male (Fox, 2002; Mitra Setia and van Schaik, 2007), which allow them to flee to this male for his (usually passive) protection in case of need, and thereby reduce harassment and the risk of infanticide. These ear-shot associations can be seen as a social counterstrategy in a situation where the likely sire is reliable in the area. In Bornean populations, no such pattern was found and lactating females even tended to avoid long calling males (Spillmann et al., 2010). Thus, females appear to avoid associations with males (Knott et al., 2018) and when in association with males, females keep their infants at close distance (Scott et al., 2019), which may indicate a residual risk of infanticide. This is not unexpected where paternity concentration is lower (as suggested by previous work), and possible sires are not reliably in the local area. However, the only report of directly observed lethal aggression in orang-utans to date was directed at an adult female and her four-year-old infant was not targeted by the attacking male at any time (for

details see Marzec et al., 2016). Thus, we would expect more promiscuous mating (sexual counterstrategies) in Bornean populations, where the social counterstrategy of ear-shot association is unlikely effective. However, in this thesis we did not find evidence for this (chapter 4), perhaps i) because Bornean females are more constrained by the ecological costs of association (chapter 3) and trade-off avoidance of male associates and paternity confusion, ii) because the unstable male dominance relationships at Suaq, Sumatra, has led to increased polyandry at Suaq (chapter 4), or iii) because of our limited data set of the Suaq population for females immediately prior to conception. Future observations are needed to resolve this uncertainty.

Conclusion on the infanticide avoidance hypothesis

To sum up, the data on orang-utan sexuality, with long periods of polyandrous mating, albeit at slow rates, concealed ovulation and mating during pregnancy is consistent with the need to confuse paternity and so reduce the risk of infanticide (chapter 4). The lack of distinct social units, and the resulting absence of permanent association with, or even proximity to, reliable protectors make the avoidance of infanticidal males particularly challenging. The wide-ranging males may be absent for years (Utami Atmoko et al., 2009b) and may suddenly show up again, which necessitates long periods of receptivity (chapter 4). The resistance to male mating initiations likewise functions to reduce infanticide risk (chapter 5). Male estimates of paternity depend on their own mating history and their assessment of other males' mating history. The more dominant a male is likely to be when the future infant is vulnerable, the more important it is to ensure he has a high estimated paternity (van Schaik et al., 2004). If this male often notices the female mating with other males, his estimate of his own likelihood of paternity will drop. Thus, by resisting mating with other males, and so recruiting the higher-ranking male, she effectively reduces the risk that the latter presents a threat to her future infant (chapter 5).

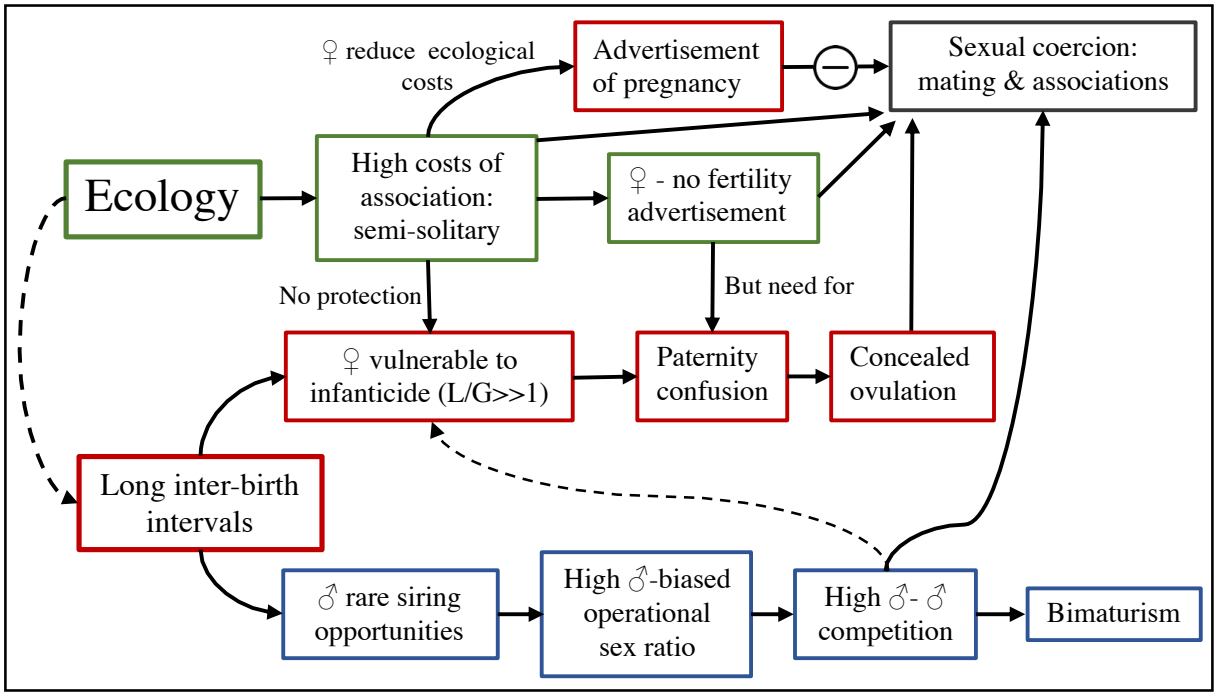

Figure 22 Scheme to summarize the patterns of sexual coercion, as forced copulations and male-maintained associations, in orang-utans, and how it may relate to ecology, the high male-biased operational sex ratio and the female counterstrategies to the risk of infanticide in a dispersed mating system (see main text for references and elaboration on the scheme). Note: the plus signs indicate increased potential for sexual coercion, whereas the minus sign proposes a mechanism for pregnant females to reduce the risk of coercion.

Our findings suggest that even though constrained by ecological costs of association, orang-utan females have evolved strategies to effectively avoid male monopolization with their concealed ovulation. The latter enables them to mate promiscuously and to exercise female choice for the most dominant male(s) and thereby reduce the risk of infanticide close to zero. Sexual coercion in the form of forced associations and copulations over an extended period is the price they pay for this effective reduction of infanticide risk (Figure 22). Previous studies have reported an enormous variability in mating frequency, coercion rates of both unflanged and flanged males, and the details of sexual interactions between study sites (e.g. for reviews: Knott, 2009; Utami Atmoko et al., 2009a). In this thesis, we investigated the mechanisms produced by colliding mating interests of males and females and could not find any evidence for different mechanisms between the populations of Suaq, Sumatra, and Tuanan, Borneo (chapter 5), when taking ecological differences and a proxy for female reproductive state into account. Suaq and Tuanan are among the most sociable populations for each of their species (Mitra Setia et al., 2009), both living in rather homogeneous, peat-swamp habitat, and so future studies will have to reveal if the patterns observed in these two populations also hold for other, less gregarious populations.

Additional future perspectives

Our results are based on observational data and unfortunately, we lack genetic paternity analyses to investigate if the predictions of the *Infanticide Avoidance Hypothesis* match on an ultimate level. Preliminary data from both study sites suggest that paternities are skewed towards flanged males at Tuanan, Borneo (Stickelberger, 2016), whereas at Suaq, Sumatra, a high paternity concentration falls on the locally dominant flanged male (Lenzi, 2014). These results match with the predictions of the *Infanticide Avoidance Hypothesis* which would predict that paternities are largely concentrated in the most dominant male(s). Interestingly, a large paternity distribution among different flanged and especially unflanged males was found in Ketambe, Sumatra, during a period of unstable male dominance relationships (Utami Atmoko et al., 2009a, 2002), suggesting some adaptation of female mating strategies to counteract the risk of infanticide during such periods. Future studies will show if such a pattern of low paternity skew, but largely concentrated on flanged males, can be found in Tuanan, Borneo, too, where male dominance relationships are generally unstable (Dunkel et al., 2013; Spillmann, 2017).

Post-copulatory mechanisms may also play a role in orang-utan reproduction. First, perhaps female resistance leads to a lower likelihood of ejaculation and thus, a lower fertilization risk for females by non-preferred males (chapter 4). Such a pattern may be difficult to investigate, however, because of visibility constraints. If the likelihood of ejaculation was reduced by female resistance, the *Infanticide Avoidance Hypothesis* would be compromised to some extent, as subordinate males would have a lower paternity estimate. However, if such scenario applied, female resistance, and thus attempts to reduce ejaculations, would be expected to be concentrated around the time of conception to avoid fertilization by a low quality male. Although we cannot conclusively dismiss effects on the ejaculation probability by female resistance, it appears unlikely to be the driving force in the light of our results (chapter 4, 5). Second, a role for sperm competition cannot be ruled out, i.e. females may incite male-male competition also by sequential polyandrous mating. Sometimes, males who displaced subordinate males copulated with the female (without resistance), too. Both testis size (Harcourt, 1997) and semen coagulation properties (i.e. sperm plug formation) are intermediate in orang-utans, similar as in humans and lower than in the highly promiscuous chimpanzees, but higher than in largely polygynous gorillas (Dorus et al., 2004), suggesting that there is at least some room, if limited, for sperm competition. Moreover, as we have shown in the fourth chapter, males cannot completely monopolize female sexuality, which further suggests some role of sperm competition (Lüpold et al., 2014). However, it is extremely challenging to investigate such post-copulatory scenarios in captivity, let alone non-invasively in the

wild. Foremost, it is crucial to evaluate paternity data to gain an idea of the ultimate perspective and evaluate the relative importance of female choice (positive and negative) and male-male competition.

"Where there is a risk of other males locating a female …, there may be strong selection for males to coerce females to mate with them as rapidly as possible" (Clutton-Brock and Parker, 1995). When there is a risk of losing sexual access to a female, orang-utan males were more prone to coerce (chapter 5) and male-male competition among flanged males was reported more likely around fertile females (Spillmann et al., 2017; Utami Atmoko et al., 2009b). Moreover, increased male: female ratios reportedly led to higher (forced) copulation rates at Gunung Palung, Borneo (Knott, 2009). Elevated male competition around a sexually active female is to be expected and in accordance with the challenge hypothesis (Wingfield et al., 1990). Higher testosterone levels of chimpanzee males in the presence of oestrous (parous) females have been reported (Muller and Wrangham, 2004; Sobolewski et al., 2013). In orang-utans, individual fluctuations of testosterone levels in response to both male-male competition and the availability of (a) fertile female(s) have not yet been investigated to our knowledge. Testosterone values are elevated during the development of the secondary sexual characteristics (Maggioncalda et al., 1999; Marty et al., 2015). It may be insightful to evaluate these physical correlates of male-male competition, such as testosterone and cortisol levels, on days with forced copulations and the presence of other males to further understand the mechanisms behind forced copulations in orang-utans.

Do forced copulations in orang-utans qualify as sexual coercion?

The definition by Smuts and Smuts (1993) has three main components i) male aggression leads to increased mating access ii) with likely fertile females and iii) females incur costs from male aggression. Smuts and Smuts (1993) themselves already admitted that their *"...definition of sexual coercion in functional as well as behavioural terms means that it may sometimes be difficult to determine whether a particular behaviour qualifies as sexual coercion"*. However, they referred to ritualized aggression which does not inflict any apparent injuries to females and discussed if this qualifies as sexual coercion. In a recent study on mountain gorillas (*Gorilla beringei beringei*), such aggressive male displays did not correlate with elevated female urinary cortisol levels (of oestrus females) and thereby, the authors concluded that male aggression towards oestrus females must be rather seen as courtship than as sexual coercion (Habumuremyi et al., 2018). Additionally, in the introduction, we discussed the difficulty of identifying male aggression that occurs decoupled from mating as sexual coercion (Baniel et al., 2017; Muller et al., 2011).

Forced copulation by orang-utan males is obviously an immediate disagreement in mating interests between the sexes. However, this conflict may be restricted to periods when a female is highly unlikely to be fertile (chapter 4), in which case forced mating would technically not qualify as sexual coercion. Even though paternity allocation data is still scarce for wild orang-utan populations, it suggests more paternities for flanged males (Banes et al., 2015; Goossens et al., 2006; Lenzi, 2014; Stickelberger, 2016; Tajima et al., 2018; Utami Atmoko et al., 2002). Unfortunately, because of the long delay between behavioural observations and opportunities to sample infant DNA, it will be difficult to link paternity data directly to behavioural data – in other words, to directly test whether and at what proportion forced copulations lead to conception or were even with fertile females. Nevertheless, the low coercion rate by flanged males, and their expected higher reproductive success indicates that forced copulations rarely lead to fertilization.

Both male mating initiations and female resistance are highly context-dependent and female sexual behaviour is congruent with a paternity confusion strategy (chapter 4 and 5). So far, no physiological costs to females directly resulting from forced copulations have been reported: Female orang-utans have never been observed to sustain physical injuries nor have elevated faecal cortisol levels been documented (although sample size issues render this negative conclusion tentative). Nonetheless, possible costs from forceful mating are diverse, ranging from constrained mate choice, to contracting

disease and more immediate stress responses (from urine) (for a review see: Knott, 2009). Such potential costs for females from forced copulations need to be evaluated in the future. Certainly, female orang-utans are not as passive as it may seem at first sight, when it comes to mating and their resistance is highly context-dependent. Females are more likely to resist if there are dominant males in vicinity. Thus, females resist, when 1) they perceive a chance of escaping the harassing male, and 2) when there is a more dominant male in the audience. Because female resistance to male mating attempts vary with the context, the question appears self-evident if such forced copulations qualify as sexual coercion. First, non-resisted copulations may still qualify as undesired by the female. After all, Parker (1979) postulated that *"if there is nothing one sex can do to avoid disadvantages inflicted by the other, then evolution simply favours making the best of things"*. The cost to the female in this case would be the fitness loss of being potentially fertilised by a non-preferred male. If this is applied to orang-utan females, it suggests that females may perceive mating initiations by males as undesired, but do not resist because they lack the context-specific incentives. Second, in more than 80% of female resisted mating initiations, males persist and force intromission despite female resistance (chapter 4). This fact strongly suggests that forced copulations should be labelled as sexual coercion. Thus, the behavioural observations make indisputably clear that there is a conflict about mating in orang-utans. The most parsimonious label for a male actively restraining a female, persisting in his mating initiation and forcing intromission remains sexual coercion.

Sexual coercion in perspective

Forced copulations in orang-utans have often been perceived as a paradox and research remained descriptive of the phenomenon itself (but see Fox, 1998, 2002; Knott, 2009; Knott et al., 2010). Forced copulations are a highly heterogeneous category, may occur in the same dyad as unforced or even cooperative copulations, and males do not inflict any apparent injuries on females (for a review: Knott, 2009). Such variation and ambiguity in sexual behaviour is exceptional in primates (also see chapter 4). We may use the link between the cost of association, female infanticide avoidance strategies and sexual coercion in orang-utans to help to integrate them into the larger evolutionary context, so as to understand the occurrence of sexual conflict and coercion in primates. So far, comparative studies have largely focused on social primate species, and orang-utans were therefore often found difficult to incorporate (but see: Emery-Thompson et al., 2008; Knott, 2009; Stumpf et al., 2008).

Orang-utans are the only nonhuman primates where forced copulations frequently occur. The question implicitly arises why this form of sexual coercion is only prevalent in two primate genera. Forced copulations are reported from various other taxa (see introduction) and thus are wide-spread in the animal kingdom (Clutton-Brock and Parker, 1995), and are an expression of an evolutionary sexual conflict over mating. However, compared to the other taxa where forced mating occurs, humans and orang-utans are unique in that females do not reliably advertise fertility and have concealed ovulation. In non-primate species female fertility is more predictable and copulations therefore more likely result in fertilization (van Noordwijk and van Schaik, 2000). Hence, in such conditions, forced copulations would translate more or less directly into reproductive success and would thus presumably be adaptive. However, in the case of catarrhine primates this relationship is more complex, because females often exhibit extended sexuality to counteract the risk of infanticide (van Schaik et al., 2000) and thus, mating may not directly be linked to fertilization (Thornhill and Gangestad, 2008). Because males likely do not have accurate cues about female reproductive status, forced copulations in orang-utans can be labelled as a short-term male strategy to directly increase mating access (Knott, 2009). Although it has been suggested that orang-utan males may also follow long-term mating strategies and thus, forced copulations may serve as intimidation or conditioning aggression, which serves to increase non-resisted mating access when the female is fertile (Wrangham and Muller, 2009), this appears highly unlikely in the light of our current findings (chapter 5).

The great ape pattern

Under the umbrella of the coevolutionary arms race resulting from the risk of infanticide, comparative approaches may help to understand when certain forms of sexual coercion occur. Because female counterstrategies to infanticide are shaped by the source of its risk (strange or familiar male, see van Schaik et al., 2004), the males' coercive strategy to control female sexuality – or more generally to get mating access – also varies with the species' socio-ecology (Clarke et al., 2009). Great apes show large variability in their socio-ecology and illustrate exactly this variation in infanticide distribution, female counterstrategies and males' attempts to control female sexuality (coercion). All great apes exhibit large sexual dimorphism (Leigh and Shea, 1995) which enables males to physically dominate females (Smuts and Smuts, 1993). However, as sociality ranges from group-living gorillas over more or less gregarious fission-fusion *Pan* species to semi-solitary orang-utans, the availability of male or female protective allies varies, leading to different dynamics of sexual conflict (reviewed in Stumpf et al., 2011). Besides the absence of seasonal breeding, great ape females vary considerably in their sexuality and how reliably they advertise fertility, which can be linked to the source of infanticide risk (van Schaik et al., 2004) and the varying cost of association in fission-fusion species (Wrangham, 2002; Surbeck, Dunkel and van Schaik, in prep.) (Figure 24). Accordingly, the prevailing forms of sexual coercion and the females' behavioural freedom also diverge among great ape species.

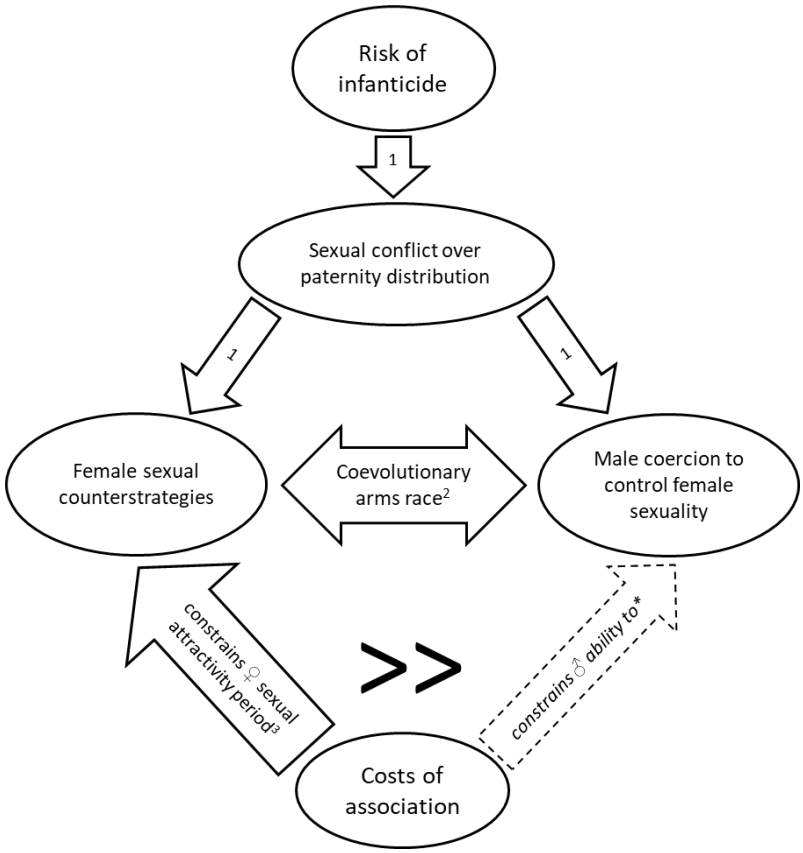

Figure 23 Illustration on how the risk of infanticide and variation in the cost of association may relate to female sexuality and male coercion patterns in fission-fusion systems (1: van Schaik et al., 2004; Clarke et al., 2009; 2: van Schaik et al., 2004; 3: Wrangham, 2002; Surbeck, Dunkel and van Schaik, in prep.; * because females' reproductive success is mostly limited by the access to resources (Emlen and Oring, 1977; Wrangham, 1979), they are more sensitive to cost of association, whereas males' benefits to associate with females, as mating opportunities, may outweigh the cost. Nevertheless, in the case of orang-utans males appear to be more constrained in their ability to monopolize access to females by the cost of association).

In group-living, polygynous gorillas, the risk of infanticide stems from immigrating males who take over the group after the death or displacement of the silverback (Robbins, 2009). Dominant males secure mating access to females, when these remain in their harem and by defending it against potential

rivals. Accordingly, male`s aggressive displays directed at females, which likely qualifies as sexual coercion, mostly occur during intergroup encounters to prevent non-fertile females from transferring into another group (Breuer et al., 2016). When females are sexually active, they do not exhibit elevated stress levels (Habumuremyi et al., 2018) despite receiving higher rates of male aggressive displays (Robbins, 2009). In this case, displays towards oestrus females rather function as consortship than coercion (Habumuremyi et al., 2018). Given that the dominant male is a good protector for the infant, the conflict about paternity allocation is relatively low between the dominant male and the female. Sexual conflict and the potential for coercive mate guarding therefore mostly arises when it comes to group choice and likely arises towards the end of a males' tenure (Manguette et al., 2019). Female counterstrategies against infanticide are of social nature (Clarke et al., 2009), such as secondary female dispersal (Manguette et al., 2019). In accordance, gorilla females do not show sexual adaptations, such as prolonged receptivity, to paternity confusion: Oestrus lasts for about 2 days only and is not reliably accompanied by sexual swellings (Watts, 1991), but proceptive mating behaviour towards the dominant male (Habumuremyi et al., 2016, 2014). However, some variation in these intersexual patterns is reported (Robbins, 2009), as some mountain gorilla groups consist of not only a single, but multiple males (Robbins and Robbins, 2018).

Female sexual counterstrategies to infanticide – and hence to male monopolization – are expected in species with multi-male-multi-female groups, where familiar, subordinate males may raise in rank and hence, pose a threat of infanticide and need some paternity probability to resume from killing an infant (e.g. concealed ovulation to achieve paternity confusion in vervets: Andelman, 1987; langurs: Heistermann et al., 2001; e.g. sexual swellings which function as graded signals to achieve multi-male mating: Nunn, 1999; Zinner et al., 2004). In fission-fusion social systems like *Pan* and *Pongo,* females additionally cannot rely on protection of their infants from continued associations with allied females or males. Furthermore, females are likely constrained by the cost of association to exhibit sexual counterstrategies to infanticide, which include extended periods of sexual attractivity ("cost-of-sexual-attraction" hypothesis: Wrangham, 2002; Surbeck, Dunkel and van Schaik, in prep.) (Figure 23). Accordingly, Wrangham (2002) proposed that the period of female sexual attractivity (i.e. swelling cycles and presumably swelling duration) negatively correlates with the costs of association and the occurrence of sexual coercion in the genus *Pan* (also see chapter 3; Figure 24). We set out to extend the first prediction of this hypothesis to *Pongo* in the third chapter and hence, to explain the absence of fertility advertisements in orang-utans. Here, we provide a precursory discussion on how the occurrence and forms of sexual coercion and the rate of infanticide relate to the varying cost of association in fission-fusion living great apes (*Pan, Pongo*) (Figure 24) and thus, attempt to fit in the orang-utans at the solitary end of this spectrum. Future work will evaluate more in detail on these patterns.

All females of the genus *Pan* exhibit large sexual swellings, go through many cycles until conception (Deschner et al., 2004; Douglas et al., 2016; Emery-Thompson and Whitten, 2003) and thus, show lengthy mating periods and mate promiscuously. Under the 'cost-of-sexual-attraction' hypothesis, lower coercion rates are expected in the more sociable population and species (Wrangham, 2002), which is generally the case (Figure 24). Bonobos (*P. paniscus*) are more gregarious than chimpanzees and feeding competition is low (Nurmi et al., 2018), with females forming alliances with other females (e.g. Tokuyama and Furuichi, 2016), having extremely extended mating periods and very low aggression rates (Hohmann and Fruth, 2003) and so far no evidence for sexual coercion by males (Paoli, 2009). Western chimpanzees (*P. troglodytes verus*) are less gregarious than bonobos, but more than the Eastern subspecies and females were reported to have prolonged mating periods (Deschner et al., 2004; Deschner and Boesch, 2007) and experience reduced coercion rates (Stumpf and Boesch, 2010, 2006, 2005). In contrast, Eastern chimpanzee (*P. troglodytes schweinfurthii*) females who face high cost of association (Emery-Thompson et al., 2014) exhibit the shortest sexually active period (less swelling cycles to conception) and frequently experience male harassment and intimidation (Muller et al., 2011, 2007). Moreover, coercive males have been reported to sire more offspring in Eastern chimpanzees (Feldblum et al., 2014). Orang-utans are at the high cost of association end (chapter 3; Figure 24), do not exhibit any morphological fertility advertisement, but have very extended mating periods with relatively frequent occurrence of forced copulations (chapter 4) and male-maintained associations

(chapter 3). The lower cost of association in Sumatran populations (*P. abelii*) may lead to higher coercion rates (Suaq: chapter 4, trend only), but females at the same time appear to rely more on social counterstrategies to infanticide by remaining in ear-shot association with the locally dominant male (Fox, 2002; Mitra Setia and van Schaik, 2007). Females of Bornean populations (*P. pygmaeus*) who were reported to hide more from males during lactational infertility (Knott et al., 2018; Spillmann et al., 2010), may thus rely less on social counterstrategies and more on comparative assessment (see first part of discussion).

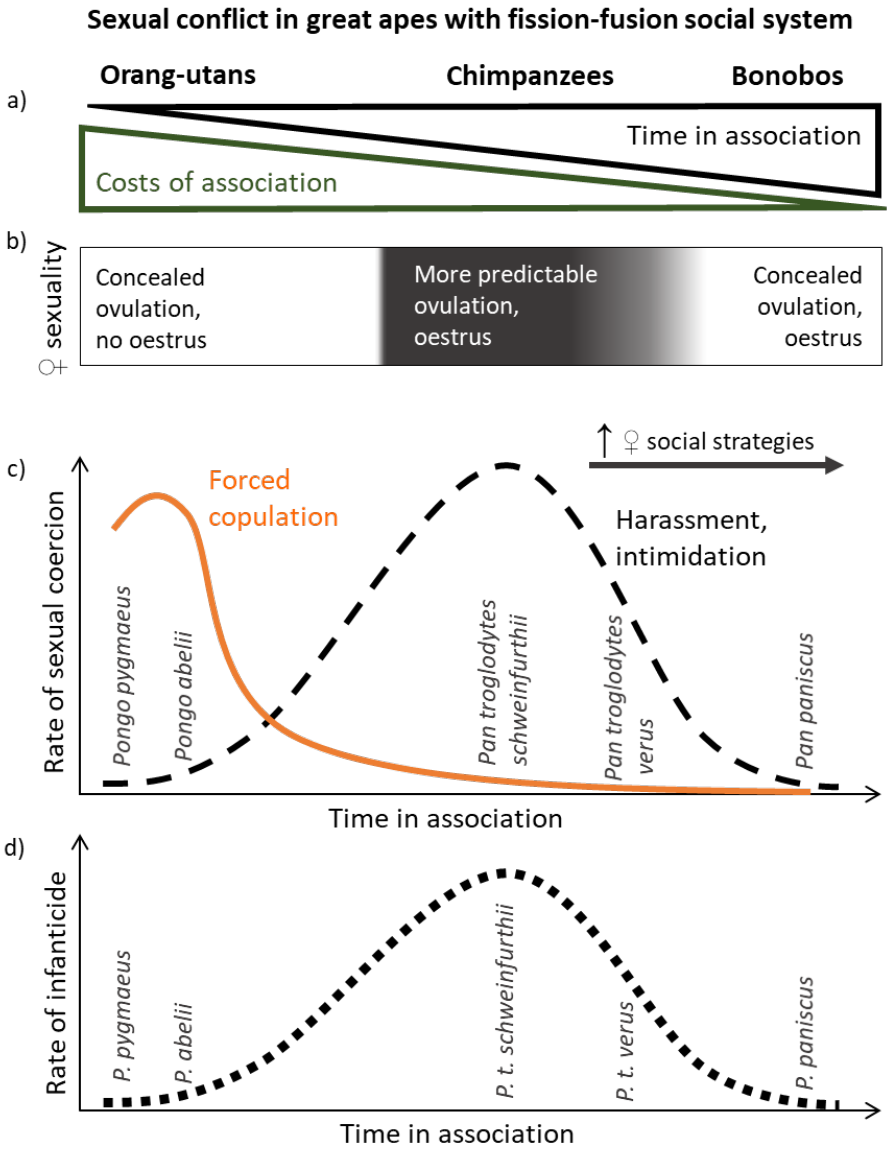

Figure 24 Tentative illustration on observed and hypothesized relationships between the time in association and a) the costs of association (*P. troglodytes schweinfurthii:* Emery-Thompson et al., 2014; *P. paniscus:* Nurmi et al., 2018; *P. troglodytes verus*: Riedel et al., 2011; *Pongo spp.*: chapter 3), b) female fertility advertisement *(P. troglodytes verus*: Deschner et al., 2004; *P. paniscus:* Douglas et al., 2016; *P. troglodytes schweinfurthii:* Emery-Thompson and Whitten, 2003; *P. abelii:* Fox, 1998; *P. pygmaeus:* Galdikas, 1981; review: Stumpf et al., 2011), c) the occurrence of sexual coercion (*P. paniscus:* Hohmann and Fruth, 2003; *P.t. schweinfurthii:* Muller et al., 2011, 2007; *P.t.verus*: Stumpf and Boesch, 2010; *Pongo spp.:* chapter 4 and 5) and d) the reported rates of infanticide (*Pongo:* Beaudrot et al., 2009; Knott et al., 2019; *Pan:* Wilson et al., 2014) in *Pongo* and *Pan* species, based on the ideas of and derived from the cost-of-sexual-attraction hypothesis (Wrangham, 2002; Surbeck, Dunkel and van Schaik, in prep.).

Because the occurrence of infanticide may be perceived as a consequence of the arms race between female social and sexual counterstrategies and male attempts to control female sexuality (Figure 23), it may provide a measure if this arms race is skewed in the favour of the female or the male (Figure 24). Eastern chimpanzee females' anti-infanticide strategies appear not as efficient as in bonobos

or Western chimpanzees and male coercion appears to skew mating patterns to the female and her offspring's disadvantage. Accordingly, reported rates of infanticide are higher in Eastern chimpanzee communities than in Western chimpanzees (Wilson et al., 2014) and infanticide has not (yet) been reported in bonobos (Hohmann et al., 2019), suggesting efficient sexual (concealed ovulation) and social counterstrategies. Although, orang-utan females appear highly constrained by cost of association, they have evolved efficient counterstrategies to infanticide (see first part of discussion), at the price of being vulnerable to forced copulations during an extended period. Although still tentative, the patterns reported suggest that the cost of association have driven interspecific variation in great apes with respect to female reproductive physiology and sexual coercion, including the risk of infanticide.

In conclusion, in both gorillas and chimpanzees, male aggression functions as a long-term intimidation strategy to achieve increased mating and siring access, whereas in orang-utans forced copulations appear to be a short-term tactic to directly increase mating access. Orang-utan males cannot rely on repeated encounters with a female when she is likely to be fertile because of the dispersed mating system and the difficulty of reliably relocating the female. The presence of concealed ovulation makes mate guarding strategies a high-cost (due to ecological constraints) and likely low-benefit tactic to males (Figure 23). Hence, orang-utan males cannot succeed in controlling a female's sexuality in the long-term and thus, resort to short-term tactics.

Comparative approach to understand sexual coercion

Humans are great apes and therefore an evolutionary link in respect to sexual coercion is expected, which makes this research topic very sensitive (reviewed in Emery-Thompson, 2009). Humans exhibit not only the largest variety of sexual coercion, including all forms described collectively for other animals – forced copulations, intimidation, and harassment (Clutton-Brock and Parker, 1995) – but also, given the general assumption of strong underreporting of cases, alarmingly high frequencies (Emery-Thompson, 2009; Wilson and Daly, 2009). Criticism of evolutionary approaches to sexual coercion in humans is often based on misunderstandings (short reviews: Wrangham and Muller, 2009; Emery-Thompson, 2009). First, we cannot argue "from is to ought", because otherwise we commit the *naturalistic fallacy*. If a behaviour can be explained from a biological point of view, and thus can be considered adaptive (Tinbergen, 1963), this by no means makes it morally or ethically justified. Second, if a biological basis can be found for sexual coercion, it does not mean that this behaviour is inevitable or even genetically determined. The behaviour displayed by any individual is the result of an interaction between genes and environment (including culture, moral considerations and legal institutions in the case of humans). Especially humans and also other great apes are known for their extraordinary behavioural flexibility (van Schaik, 2016), which further supports that behavioural patterns, even if they have a biological basis, can be modified or suppressed dependent on prevailing conditions. Our results on orang-utan sexuality presented in this thesis are the best example of how flexibly behavioural patterns change in nonhuman great apes.

Of course, the factors affecting human behavioural patterns are very complex and diverse. Different nonhuman primate species do not come close to this social and cultural complexity, thus hampering the value of comparative studies. Nevertheless, evaluating an evolutionary perspective may help to identify the biological risk factors which lead to coercion, contribute to grasp why its frequency is so high, and eventually result in interdisciplinary approaches to reduce sexual coercion in human societies (Rosenfeld, 2009). It is not in the scope of this thesis to elaborate more on such comparative approaches, but by evaluating the orang-utan pattern we provided yet another puzzle piece to understand when females are at risk of coercion.

Conclusion

With this thesis, we provide an integrative approach to understand the frequent occurrence of sexual coercion in orang-utans by placing it into the context of their socio-ecology and the underlying sexual conflict. We found that forced copulations are not an individual male trait, a dyad-specific phenomenon, or a male morph-specific reproductive tactic, but can only be understood in the light of the immediate social context, i.e. the potential for male competition, and the female's need for infanticide avoidance strategies. Both female sexuality (concealed ovulation leading to prolonged mating periods) and female mating behaviour (proceptivity and resistance) are consistent with paternity confusion and thus ultimately may serve infanticide avoidance. Males appear to initiate mating when they perceive mating competition and thus when they are at risk of being displaced from mating access, and this is exactly the time that females are most likely to resist such attempts. However, the orang-utan mating system remains incompletely understood. As a result of their semi-solitary lifestyle and slow life history, acquiring sufficiently large sample sizes which allow conclusive inferences is difficult. Only the analysis of long-term data from several study sites can help to understand the mating tactics of these evasive apes and especially how patterns vary with socio-ecological factors. With this study, we emphasize the variability of both male and female mating tactics and accordingly, the context-dependency of mating conflict.

The insight we provide into sexual conflict in orang-utans may help to understand the biological factors behind the evolution of sexual coercion in future comparative work. The observation of non-human primates provides additional information on sexual behaviour and sexual coercion, which is less distorted by reporting bias. Therefore, nonhuman primates may help us to assess under which circumstances specific forms of sexual coercion occur and finally contribute to evaluating risk factors which make females vulnerable to coercion. Once future work will have provided us with a more complete framework for predicting the various forms of sexual coercion, the results may inform attempts to reduce sexual assaults in human societies.

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Appendix

Chapter 2: Male Alternative Reproductive Tactics

The model outputs for the analyses reported in the results, which are not reported as tables in the main text, are reported here.

Association frequency – cross-sectional data

Stable 1 Association frequency of unflanged and flanged males: Poisson GLMM output for the number of female associates per male full-day focal follow (N=807) by individual (N=92) and follow periods (N=317) depending on male morph, study site and fruit availability ($\chi^2_{3,6}$ = 60.53, P<0.0001, AIC=1208.8, pseudo-R^2 = 0.19). Fixed factors with P<0.05 are indicated in bold.

	Estimate	SE	z value	P value
Intercept	*-1.170*	*0.209*	–	–
Site (Suaq vs. Tuanan)	-0.323	0.211	-1.531	0.126
Male morph (unflanged vs. flanged)	-1.087	0.143	**-7.607**	**<0.001**
z Fruit Availability Index	0.138	0.065	**2.128**	**0.033**

Stable 2 Association pattern difference between unflanged and flanged males: LMM output for a) the duration of male-female associations (h) and b) the time spent in proximity (<10m) during these associations depending on study site, male morph, female class and zFAI. (*Note* the sample sizes are not the same in the two models, because for some data the proximity measurements were not available. Furthermore, only male identity was included as a random intercept in the proximity analyses, because otherwise the model would not have converged. However, the null-model was not improved, when including the dyad and the female identity as a random intercept ($\chi^2_{3,5}$= 2.502, P=0.29, AIC=610.72). Fixed factors with P<0.05 are indicated in bold.

Response *Model comparison* *Sample sizes*	**Fixed effects**	**Estimate**	**SE**	**t value**	**P value**
a) Association duration (h)	*Intercept*	*0.917*	*0.159*	–	–
	Site (Suaq vs. Tuanan)	0.089	0.157	0.563	0.575
$\chi^2_{5,10}$=25.678, P=0.0001,	Male morph (unflanged vs. flanged)	-0.597	0.161	-3.694	<0.001
pseudo-R^2=0.21	Female parity (nulliparous vs. parous)	-0.480	0.133	-3.613	<0.001
	z Fruit Availability Index	-0.056	0.036	-1.574	0.116
N=1457, 622 dyads, 219 male IDs, 66 female IDs	**Male morph : Female parity**	0.389	0.174	**2.236**	**0.026**
b) Proportion in proximity (<10m) to female	*Intercept*	*0.299*	*0.023*	–	–
	Site (Suaq vs. Tuanan)	0.175	0.021	**8.516**	**<0.001**
$\chi^2_{3,7}$=123.59, P<0.0001,	**Male morph (unflanged vs. flanged)**	-0.184	0.018	**-10.202**	**<0.001**
N=1324, 203 male IDs	Female parity (nulliparous vs. parous)	-0.002	0.019	-0.090	0.928
	z Fruit Availability Index	0.018	0.008	**2.159**	**0.031**

Because female orang-utans do not exhibit any apparent signal of fertility and/or cycling activity like other primates (Nunn, 1999; Zinner et al., 2004) and inter-birth intervals are highly variable in length, it remains difficult to assess a female's reproductive status in the wild (also see Knott et al., 2009; chapter 4), without female reproductive hormone measures. One proxy for parous females' reproductive state is the age of her dependent offspring (Fox, 1998). Because this indirect measure can only be used for parous females, we report this separate analysis for the association duration between parous females and both unflanged and flanged males, including the females' reproductive state (age of the dependent offspring) (Stable 3). Males associate longer with females with older offspring (Stable 3).

Stable 3 Association duration with parous females: Linear Mixed Model (LMM) for the total duration (hours) of male-female associations only including parous females with dependent offspring depending on study site, male morph, female reproductive state (i.e. age of the dependent offspring) and fruit availability (N=945 dyadic associations of 373 different dyads including 174 male IDs and 31 female IDs, $\chi^2_{5,10}$ = 30.7, P<0.0001, AIC=3146.0, pseudo-R^2=0.19).

	Estimate	SE	t value	P value
Intercept	*0.429*	*0.140*	–	–
Site (Suaq vs. Tuanan)	-0.262	0.149	-1.760	0.095
Age of dependent offspring (y)	0.093	0.021	**4.503**	**<0.001**
Male morph (unflanged vs. flanged)	-0.257	0.098	-2.613	0.010
z Fruit Availability Index (FAI)	0.084	0.059	1.418	0.157
Male morph (unflanged vs. flanged) : z FAI	-0.264	0.086	**-3.083**	**0.002**

Longitudinal patterns

Stable 4 Within-individual behavioural changes with the development of SSC: Output of the models assessing within-individual differences between the unflanged to the flanged male morph in respect to the a) association proportion with females (of all observation hours), b) proportion of association time in close proximity to females (<10m) and c) the total number of copulations per observation hour. All fixed effects with P<0.05 are indicated in bold. Model comparisons to the null model, including random intercepts only, are reported below the response. (*Note:* For a) and c) "quasi-Poisson" generalized linear models [GLM] were conducted to assess the changes within individual depending on their male morph [N=12 of 6 males] with the observation time as an offset. There was only one male included from the Suaq population [Xenix] and therefore, no site differences could be assessed. Excluding Xenix did not lead to different results [see suppl. mat.]. *Note:* §= the sample size for the proximity to females during associations is larger, because also males that were followed for less than 100 focal hours per morph state were included in this analysis)

Model	Response *(comparison to null model)*	Fixed effect	Estimate	SE	t value	P value
GLMM	**Number of female associates** $\chi^2_{3,6}$= *31.50, P<0.0001 N=250 days of 6 IDs and 82 follow periods*	*Intercept*	*-0.232*	*0.630*	–	–
		Site (Suaq vs. Tuanan)	-0.198	0.644	-0.308	0.758
		Male morph (unflanged vs. flanged)	-1.170	0.230	**-5.086**	**<0.001**
		z Fruit Availability Index	0.186	0.106	1.759	0.079
LM	**Association proportion** $F_{1,10}$=*13.55, P=0.004 N=12 (6 IDs)*	*Intercept*	*0.510*	*0.070*	–	–
		Male morph (unflanged vs. flanged)	-0.363	0.099	**-3.681**	**0.004**
LMM	**Proportion in proximity to female (<10m)** $\chi^2_{6,7}$=*5.17, P=0.02, N=16 of 8 IDs*§	*Intercept*	*0.332*	*0.071*	–	–
		Site (Suaq vs. Tuanan)	0.103	0.080	1.296	0.226
		Male morph (unflanged vs. flanged)	-0.164	0.063	**-2.600**	**0.028**
		z Association hours with females	0.027	0.036	0.764	0.458
GLM	**Copulation frequency** χ^2_1=*117.34, P<0.0001 N=12 (6 IDs)*	*Intercept*	*-3.685*	*0.225*	–	–
		Male morph (unflanged vs. flanged)	-4.921	1.309	**-3.760**	**0.004**
		z Association hours with females	0.078	0.066	1.192	0.264

Stable 5 Model outputs of the within individual analysis without Xenix (only Suaq male available) (N=10 of 5 males)

Model	Response	Fixed effect	Estimate	SE	t value	P value
LM	**Association rate** $F_{1,8}$=23.32, P=0.001	*Intercept*	*0.466*	*0.056*	–	–
		Male morph (unflanged vs. flanged)	-0.380	0.079	**-4.829**	**0.001**
GLM	**Copulation frequency** χ^2_1=96.02, P<0.00001	*Intercept*	*-3.857*	*0.206*	–	–
		z Association hours with adult females	0.121	0.058	2.107	0.073
		Male morph (unflanged vs. flanged)	-4.723	1.078	**-4.381**	**0.003**

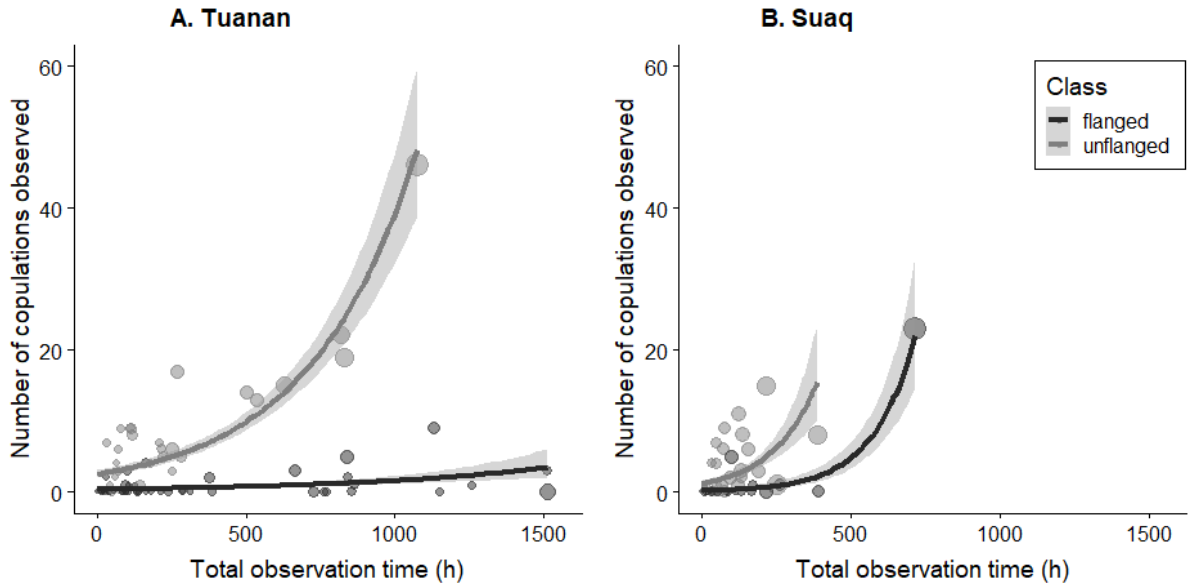
Copulation frequency – cross-sectional data

Stable 6 Copulation frequency: Poisson GLMM output for the total number of copulations observed by individual males and their morph (N=66 of 58 different individuals). Total observation time was an offset term, male identity a random intercept. Only males (and morph) for which at least 100 hours of observation time were available, were included ($\chi^2_{2,5}$=121.4, P<0.0001, pseudo-R^2=0.95). All fixed effects with P<0.05 are indicated in bold. (*Note:* Islo, the dominant flanged male of Suaq, is included in this analysis. The model output without Islo is reported in the supplementary material)

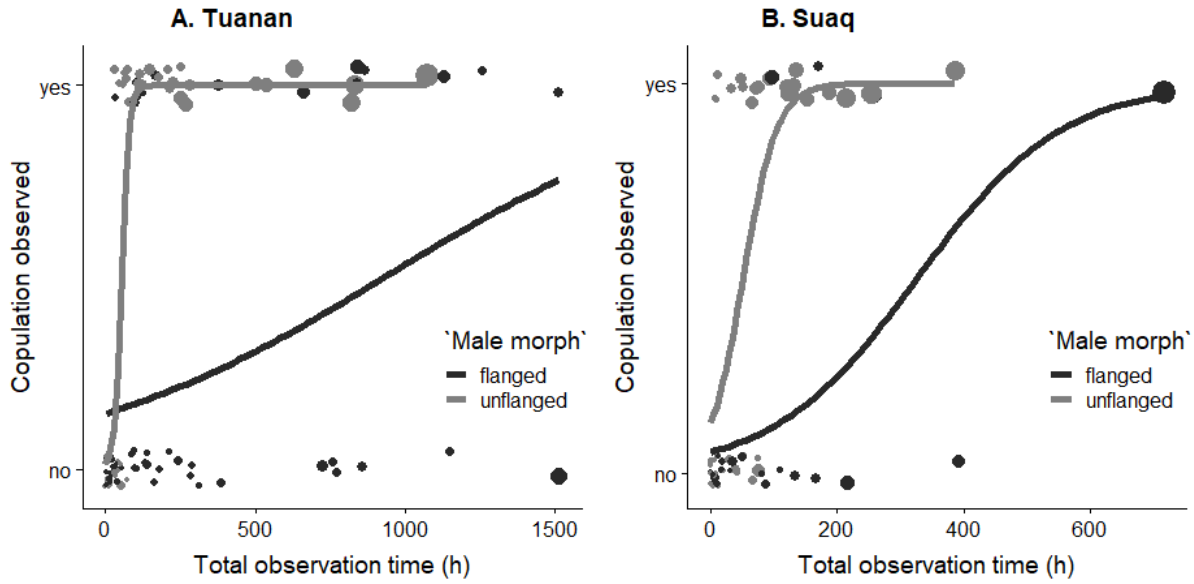
	Estimate	SE	z value	P value
Intercept	*-6.263*	*0.373*	–	–
Site (Suaq vs. Tuanan)	-0.093	0.333	-0.279	0.780
Male morph (unflanged vs. flanged)	-2.775	0.299	**-9.269**	**<0.001**
z Association hours with females	0.229	0.114	**2.007**	**0.045**

Stable 7 Copulation frequency: Poisson GLMM (excluding Islo, the dominant flanged male of Suaq) for the number of copulations observed for each male individual by male morph (flanged vs. unflanged), site (Suaq vs. Tuanan) and total time spent in association with adult females (i.e. copulation opportunities) ($\chi^2_{3,5}$=130.4, P<0.0001, R^2=0.62, N=65 of 57 males).

	Estimate	SE	z value	P value
Intercept	*-3.664*	*0.266*	–	–
Site (Suaq vs. Tuanan)	0.202	0.316	0.639	0.523
Male morph (unflanged vs. flanged)	-2.927	0.287	**-10.191**	**<0.001**
z Association hours with adult females	0.122	0.103	1.183	0.237



Sfigure 1 Number of observed copulations by individual and male morph (unflanged and flanged) depending on the total observation hours available for this individual for both study sites (left: Tuanan (flanged: N=54; unflanged: N=39), right: Suaq (flanged: N=23; unflanged: N=43)). The size of the data points is relative to the association hours with adult females. Smoothing lines following a Poisson glm function ('ggplot2' package) are shown to illustrate the trends. (Note: The flanged male in Suaq on the far right is Islo, the dominant male from 2007 to 2014).



Sfigure 2 Copulation occurrence as a function of observation time based on individual males by study site (A: Tuanan, B: Suaq) and male morph (dark: flanged; light grey: unflanged males).

Coercion frequency – cross-sectional data

The analyses were conducted twice – once with the male who had developed his SSCs during the study period included in the unflanged morph (Stable 8) and once in the flanged morph (Stable 9). Although patterns were the same, both analyses are reported here.

Stable 8 Coercion frequency of individual males: Output of the quasi-binomial GLM for the proportion of forced copulations by individual males (N=65) by study site, male morph and association hours with females (z-transformed). The total observation time was included as a weighting variable. The male who developed his SSCs during the study period was included only in his unflanged morph. *Note:* Both the model excluding and including the interaction term are reported. The likelihood ratio test reported below the model output relates to the model reported on top.

	Estimate	**SE**	**t value**	**P value**
Intercept	0.230	0.327	-	-
Site (Suaq vs. Tuanan)	-0.812	0.344	**-2.360**	**0.022**
Male morph (unflanged vs. flanged)	-1.705	0.363	**-4.694**	**<0.001**
z Association hours with females	-0.018	0.055	-0.327	0.745
Comparison to the null model: χ^2_3=12619, P<0.0001				
Intercept	1.013	0.346	-	-
Site (Suaq vs. Tuanan)	-1.927	0.393	-4.908	<0.001
Male morph (unflanged vs. flanged)	-4.015	0.688	-5.833	<0.001
z Association hours with females	0.058	0.049	1.184	0.241
Site : Male morph	3.403	0.776	**4.385**	**<0.001**
Comparison to the null model: χ^2_4=19903, P<0.0001				
Comparison to the full model without interaction terms: χ^2_1=7283, P<0.0001				

Stable 9 Coercion frequency of individual males: Output of the quasi-binomial GLM for the proportion of forced copulations by individual males (N=65) by study site, male morph and association hours with females (z-transformed). The total observation time was included as a weighting variable. The male who developed his SSCs during the study period was included only in his flanged morph. *Note:* Both the model excluding and including the interaction term are reported. The likelihood ratio test reported below the model output relates to the model reported on top.

	Estimate	**SE**	**t value**	**P value**
Intercept	0.255	0.328	–	–
Site (Suaq vs. Tuanan)	-0.795	0.346	**-2.297**	**0.025**
Male morph (unflanged vs. flanged)	-1.748	0.363	**-4.812**	**<0.001**
z Association hours with females	-0.026	0.057	-0.452	0.653
Comparison to the null model: χ^2_3=13243, P<0.0001				
Intercept	1.013	0.350	–	–
Site (Suaq vs. Tuanan)	-1.921	0.403	-4.768	<0.001
Male morph (unflanged vs. flanged)	-4.013	0.695	-5.774	<0.001
z Association hours with females	0.057	0.052	1.103	0.274
Site : Male morph	3.357	0.788	**4.258**	**<0.001**
Comparison to the null model: χ^2_4=20199, P<0.0001				
Comparison to the full model without interaction terms: χ^2_1=6955, P<0.0001				

Chapter 3: The Cost of Association

Activity budget changes

Active time

Stable 10 LMM output for daily active time (hours) variation by social, ecological and physiological factors ($\chi^2_{4,16}$=108.02, P<0.001, ΔAIC= 84.01, N=2086; 20 IDs and 279 FPs). Social factors improved control model significantly ($\chi^2_{8,16}$ =56.27, P<0.001, ΔAIC=40.27), whereas there was no improvement when adding an interaction term with site and time in association with males or females ($\chi^2_{16,18}$=0.49, P=0.78, ΔAIC =3.51). (*Note:* fixed effect variable was z-transformed prior to analysis; C=Control factor, F= fixed effect)

		Estimate	SE	t value	P value
Intercept		11.093	0.153	-	-
Site (Suaq vs. Tuanan)	C	-0.171	0.169	-	-
z Cumulative female association hours	F	0.084	0.024	**3.441**	**0.001**
z Cumulative male association hours	F	0.071	0.034	**2.102**	**0.036**
Number of copulations	F	-0.025	0.132	-	-
Male-female cumulative aggression index	F	0.024	0.089	0.267	0.789
Female-female agonistic interactions (no vs. yes)	F	-0.323	0.200	-1.612	0.107
z Fruit Availability Index	C	0.093	0.039	**2.404**	**0.017**
z Age of dependent offspring (y)	C	0.067	0.042	1.582	0.115
Social interaction time (h)	C	0.554	0.155	**3.580**	**<0.001**
Consecutive days with female count	F	0.052	0.045	1.160	0.246
Consecutive days with male count	F	0.057	0.024	**2.420**	**0.016**
Site : Number of copulations	F	0.417	0.155	**2.694**	**0.007**

Because the active time increased with several social factors (Stable 10), we assessed if and how the different activities changed relative to this increased active time (Stable 11) and how the activity budget changed absolutely (Stable 12).

Feeding time

The full model for daily feeding time including the interaction terms between social factors and the study site was significantly better than the control model ($\chi^2_{8,18}$=132.2, P<0.0001, ΔAIC=112.19) (Stable 11) and, than the one excluding the interactions. Daily female feeding time (hours) decreased significantly more in the less sociable population of Tuanan, when females were in association with either adult females (β=-0.283±0.061, t=-4.661, P<0.0001) or males (β=-0.205±0.082, t=-2.489, P=0.01) compared to the more sociable population of Suaq (Stable 11; Sfigure 3). Moreover, on days with copulations the feeding time of females was reduced at Tuanan, but not at Suaq (β=-0.611±0.225, t=-2.721, P=0.007) (Sfigure 4). There was no effect on feeding time on days with aggression received neither from males nor females (Stable 11). Neither the Fruit Availability Index nor the age of the dependent infant had an effect on the feeding time of females (Stable 11). In sum, the variation in daily feeding time was best predicted by social factors, whereas social factors affected feeding time more in the population of Tuanan than Suaq.

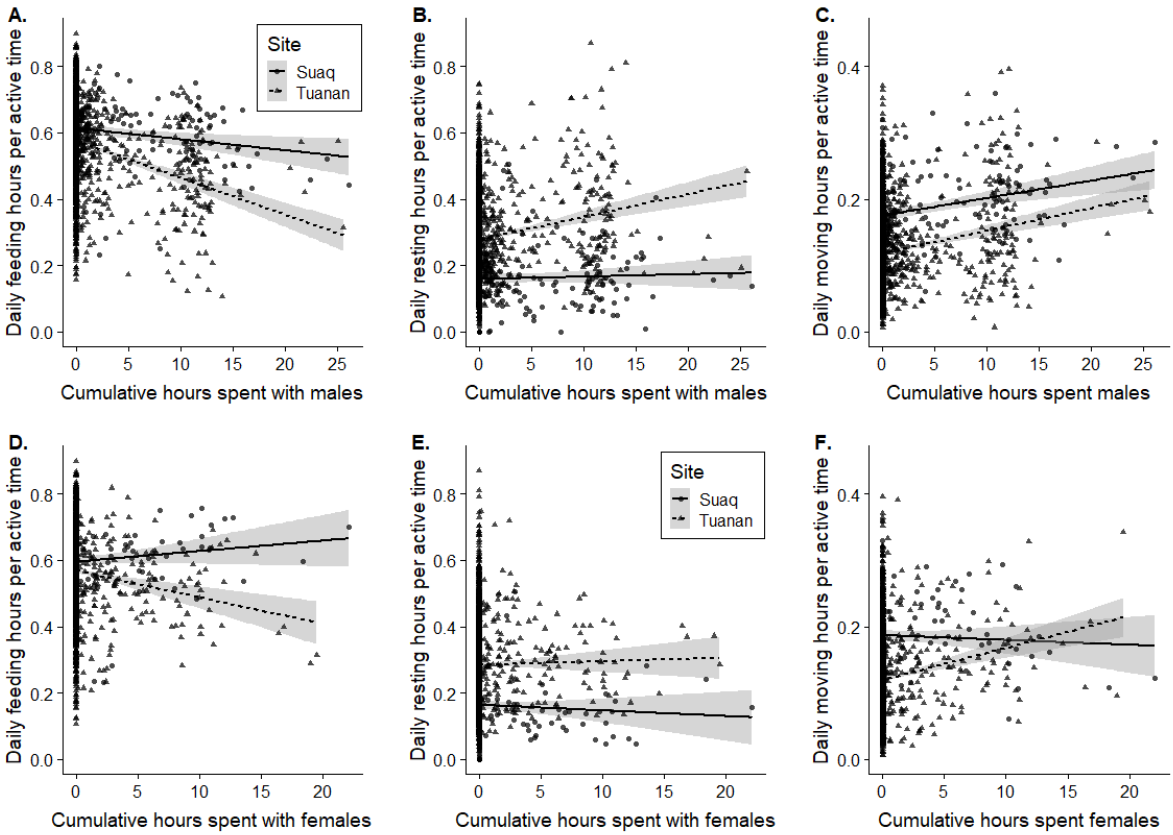
Moving time

For the time spent moving, the model fit was not improved by adding social factors into the control model ($\chi^2_{8,15}$=12.27, P=0.09, ΔAIC=1.7) (Stable 11). Also it was not improved by adding any interaction term between social factors and study site ($\chi^2_{15,20}$=3.25, P=0.35, ΔAIC=2.8). Because moving time and day journey length generally increase with increasing active time (Ashbury et al., 2020) and

daily active time was set as the offset term in the model, we could not find any effect of social factors on moving time, besides the total social interaction time. Daily active time varied with social factors, and especially increased with association time (Stable 10).

Resting time

Overall, the full model for daily resting time containing all the social factors and the interaction terms with the study site was significantly better than the control model ($\chi^2_{8,16}$=23.85, P=0.002, ΔAIC=7.85; Stable 11). Resting time increased significantly more at Tuanan in response to associations with males than at Suaq (β=0.178±0.085, t=2.090, P=0.04) (Stable 11; Sfigure 3). As more days were spent in association with males, daily resting time decreased (β=-0.107±0.034, t=-3.184, P=0.001). Conversely, with increasing time in association with other females, females rested less (Stable 11). Even though resting time seemed to increase with the occurrence of copulations (Sfigure 4), we did not detect any statistical evidence for it (Stable 11). However, females tended to rest more on days with male-female aggression (β=0.213±0.126, t=1.689, P=0.09), but not on days with female-female aggression (Stable 11).



Sfigure 3 Daily activity budget changes (feeding (A, D), resting (B, E) and moving (C, F) hours [per total active hours]) depending on the cumulative hours spent in association with males (*top row:* A, B, C) and with females (*bottom row:* D, E, F) by study site (circle: Suaq; triangle: Tuanan). Data points are based on full-day focal follows of parous females from follow periods of at least 5 days. *Note:* The lines indicate the correlation between the activity and the time spent with males/females, but not the model predictions.

Stable 11 LMM outputs of the full models for daily feeding, moving and resting hours of parous females (N=2086 full-day follows of 20 parous females and 279 follow periods). Daily active time was included as an offset term in all the models. The comparison of each full model (reported model) to the control model is reported in the first column below the response variable. All fixed and control effects with P<0.05 are indicated in bold. (*Note:* z = fixed effect variable was z-transformed prior to analysis; O= offset term; C=Control factor, F= fixed effect).

Response	Fixed effects		Estimate	SE	t value	P value
Feeding hours	Intercept	I	-4.414	0.264	-	-
	Active Time (h)	*Offset*				
	Site (Suaq vs. Tuanan)	C	-0.507	0.300	-	-
$\chi^2_{8,18}$=132.2, P<0.001, ΔAIC=112.19	z Cumulative female association hours	F	0.097	0.054	-	-
	z Cumulative male association hours	F	-0.136	0.069	-	-
	Consecutive days with female count	F	-0.148	0.061	**-2.438**	**0.015**
	Consecutive days with male count	F	0.012	0.032	0.389	0.697
	Number of copulations	F	0.093	0.184	-	-
	Male-female cumulative aggression index	F	-0.157	0.122	-1.293	0.196
	Female-female agonistic interactions (no vs. yes)	F	-0.095	0.270	-0.353	0.724
	z Fruit Availability Index	C	-0.095	0.052	-1.844	0.066
	z Age of dependent offspring (y)	C	0.016	0.058	0.285	0.776
	Social interaction time (h)	C	-1.522	0.209	**-7.286**	**<0.001**
	Site : z Cumulative female association hours	F	-0.283	0.061	**-4.661**	**<0.001**
	Site : z Cumulative male association hours	F	-0.205	0.082	**-2.489**	**0.013**
	Site : Number of copulations	F	-0.611	0.225	**-2.721**	**0.007**
Moving hours	Intercept	I	-9.209	0.158	-	-
	Active Time (h)	*Offset*				
	Site (Suaq vs. Tuanan)	C	-0.399	0.178	**-2.242**	**0.038**
$\chi^2_{4,8}$=23.17, P<0.001, ΔAIC=15.2	**Social interaction time (h)**	C	-0.648	0.156	**-4.158**	**<0.001**
	z Fruit Availability Index	C	0.048	0.037	1.289	0.198
	z Age of dependent offspring (y)	C	0.041	0.040	1.025	0.306
Resting hours	Intercept	I	-9.268	0.300	-	-
	Active Time (h)	*Offset*				
	Site (Suaq vs. Tuanan)	C	1.605	0.338	-	-
$\chi^2_{8,16}$=23.85, P=0.002, ΔAIC=7.85	z Cumulative female association hours	F	-0.035	0.035	-1.023	0.306
	z Cumulative male association hours	F	0.042	0.072	-	-
	Consecutive days with female count	F	0.048	0.064	0.751	0.453
	Consecutive days with male count	F	-0.107	0.034	**-3.184**	**0.001**
	Number of copulations	F	-0.152	0.144	-1.058	0.290
	Male-female cumulative aggression index	F	0.213	0.126	1.689	0.091
	Female-female agonistic interactions (no vs. yes)	F	0.404	0.283	1.426	0.154
	z Fruit Availability Index	C	-0.137	0.064	**-2.149**	**0.032**
	z Age of dependent offspring (y)	C	-0.240	0.072	**-3.316**	**0.001**
	Social interaction time (h)	C	0.022	0.220	0.100	0.920
	Site: z Cumulative male association hours	F	0.178	0.085	**2.090**	**0.037**

Stable 12 LMM outputs of the full models for daily feeding, moving and resting hours of parous females (N=2086 full-day follows of 20 parous females and 279 follow periods) excluding daily active time as offset term. The comparison of each full model (reported model) to the control model is reported in the first column below the response variable. All fixed and control effects with P<0.05 are indicated in bold. (*Note:* z = fixed effect variable was z-transformed prior to analysis; O= offset term; C=Control factor, F= fixed effect).

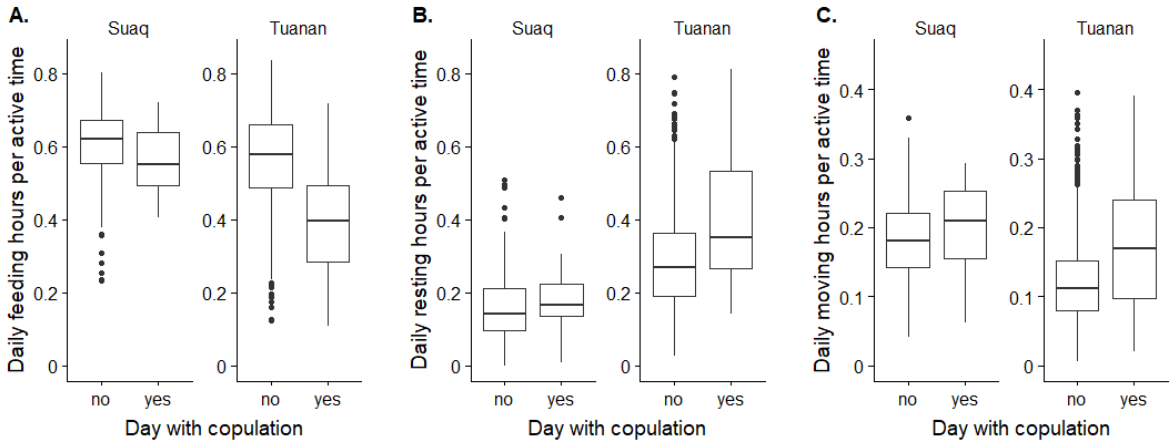
Response	Fixed effects		Estimate	SE	t value	P value
Feeding hours	Intercept	I	6.772	0.256	-	-
	Site (Suaq vs. Tuanan)	C	-0.718	0.286	-	-
	z Cumulative female association hours	F	0.166	0.055	-	-
$\chi^2_{8,17}$=54.18,	z Cumulative male association hours	F	-0.062	0.069	-	-
P<0.001,	Consecutive days with female count	F	-0.100	0.062	-1.620	0.105
ΔAIC=36.18	**Consecutive days with male count**	F	0.069	0.033	**2.102**	**0.036**
	Number of copulations	F	-0.032	0.139	-0.231	0.817
	Male-female cumulative aggression index	F	-0.107	0.122	-0.875	0.381
	Female-female agonistic interactions (no vs. yes)	F	-0.447	0.275	-1.627	0.104
	z Fruit Availability Index	C	-0.003	0.058	-0.047	0.962
	z Age of dependent offspring (y)	C	0.097	0.065	1.495	0.136
	Social interaction time (h)	C	-1.014	0.213	**-4.758**	**<0.001**
	Site : z Cumulative female association hours	F	-0.259	0.062	**-4.179**	**<0.001**
	Site : z Cumulative male association hours	F	-0.215	0.081	**-2.643**	**0.008**
Moving hours	Intercept		1.962	0.090	-	-
	Site (Suaq vs. Tuanan)	F	-0.620	0.096	-	-
	z Cumulative female association hours	F	-0.018	0.024	-	-
$\chi^2_{8,17}$=63.39,	**z Cumulative male association hours**	F	0.049	0.021	**2.348**	**0.019**
P<0.001,	**Consecutive days with female count**	F	0.063	0.027	**2.281**	**0.023**
ΔAIC=45.39	**Consecutive days with male count**	F	0.031	0.015	**2.111**	**0.035**
	Number of copulations	F	0.014	0.081	0.170	0.865
	Male-female cumulative aggression index	F	-0.076	0.055	-1.380	0.168
	Female-female agonistic interactions (no vs. yes)	F	0.093	0.122	0.765	0.444
	z Fruit Availability Index	C	0.154	0.026	**5.962**	**<0.001**
	z Age of dependent offspring (y)	C	0.130	0.029	**4.556**	**<0.001**
	Social interaction time (h)	C	0.023	0.095	0.243	0.808
	Site : z Cumulative female association hours	F	0.080	0.027	**2.929**	**0.003**
	Site : Copulation count	F	0.197	0.097	**2.039**	**0.042**
Resting hours	Intercept	I	1.956	0.297	-	-
	Site (Suaq vs. Tuanan)		1.427	0.340	-	-
	z Cumulative female association hours		-0.054	0.052	-	-
$\chi^2_{8,17}$=64.85,	z Cumulative male association hours		0.059	0.064	-	-
P<0.001,	Consecutive days with female count	F	0.077	0.058	1.365	0.172
ΔAIC=46.85	Consecutive days with male count	F	-0.050	0.030	-1.683	0.093
	Number of copulations	F	0.100	0.129	0.466	0.641
	Male-female cumulative aggression index	F	0.256	0.113	**2.019**	**0.044**
	Female-female agonistic interactions (no vs. yes)	F	0.022	0.257	0.121	0.903
	z Fruit Availability Index	C	-0.053	0.050	-1.095	0.274
	z Age of dependent offspring (y)	C	-0.150	0.055	**-2.835**	**0.005**
	Social interaction time (h)	C	0.522	0.198	**2.586**	**0.010**
	Site : z Cumulative female association hours	F	0.147	0.058	**2.521**	**0.012**
	Site : z Cumulative male association hours	F	0.252	0.074	**3.113**	**0.002**

Stable 13 LMM output of the full models for activity budget changes of parous females at Tuanan in response to social, ecological and physiological factors (N=1874 full day follows of 15 females and 250 FPs). Fixed factors with P<0.05 are indicated in bold. Below the response variable the model comparison is reported based on likelihood ratio tests.

Reponse	Fixed Effects	Type	Estimate	SE	t value	P value
Active hours	Intercept		10.943	0.083		
	z Cumulative female association hours	Fixed	0.088	0.029	**3.046**	**0.002**
$\chi^2_{4,14}$= 94.28, P<0.01, ΔAIC=74.28	**z Cumulative male association hours**	Fixed	0.084	0.043	**1.951**	**0.051**
	Number of copulations	Fixed	0.336	0.132	**2.551**	**0.011**
	Male-female cumulative aggression index	Fixed	0.029	0.116	0.254	0.800
	Female-female agonistic interactions (no vs. yes)	Fixed	-0.318	0.213	-1.495	0.135
	z Fruit Availability Index	Control	0.144	0.043	**3.374**	**0.001**
	z Age of dependent offspring (y)	Control	0.085	0.047	1.807	0.072
	Social interaction time (h)	Control	0.593	0.171	**3.474**	**0.001**
	Consecutive days with female count	Fixed	0.054	0.051	1.064	0.287
	Consecutive days with male count	Fixed	0.037	0.029	1.282	0.200
Feeding hours	Intercept		-4.907	0.141		
	Active time (h)	Offset				
	z Cumulative female association hours	Fixed	-0.169	0.039	**-4.299**	**<0.001**
$\chi^2_{4,14}$=233.64, P<0.001, ΔAIC=213.64	**z Cumulative male association hours**	Fixed	-0.337	0.058	**-5.823**	**<0.001**
	Number of copulations	Fixed	-0.492	0.179	**-2.746**	**0.006**
	Male-female cumulative aggression index	Fixed	-0.146	0.158	-0.929	0.353
	Female-female agonistic interactions (no vs. yes)	Fixed	-0.102	0.289	-0.352	0.725
	z Fruit Availability Index	Control	-0.146	0.056	**-2.592**	**0.010**
	z Age of dependent offspring (y)	Control	0.006	0.062	0.096	0.923
	Social interaction time (h)	Control	-1.651	0.232	**-7.110**	**<0.001**
	Consecutive days with female count	Fixed	-0.191	0.069	**-2.742**	**0.006**
	Consecutive days with male count	Fixed	0.017	0.039	0.444	0.657
Moving hours	Intercept		-9.614	0.095		
	Active time (h)	Offset				
$\chi^2_{4,7}$ =18.66, P<0.001, ΔAIC=12.66	z Fruit Availability Index	Fixed	0.014	0.041	0.333	0.740
	z Age of dependent offspring (y)	Fixed	0.026	0.044	0.598	0.550
	Social interaction time (h)	Fixed	-0.732	0.170	**-4.296**	**<0.001**
Resting hours	Intercept		-7.683	0.166		
	Active time (h)	Offset				
$\chi^2_{4,14}$=30.71, P<0.001, ΔAIC=10.81	z Cumulative female association hours	Fixed	-0.012	0.041	-0.301	0.764
	z Cumulative male association hours	Fixed	0.203	0.063	**3.238**	**0.001**
	Number of copulations	Fixed	-0.114	0.189	-0.606	0.545
	Male-female cumulative aggression index	Fixed	0.210	0.166	1.270	0.204
	Female-female agonistic interactions (no vs. yes)	Fixed	0.385	0.302	1.273	0.203
	z Fruit Availability Index	Control	-0.194	0.070	**-2.780**	**0.006**
	z Age of dependent offspring (y)	Control	-0.225	0.078	**-2.899**	**0.004**
	Social interaction time (h)	Control	0.114	0.244	0.466	0.641
	Consecutive days with female count	Fixed	0.076	0.073	1.044	0.297
	Consecutive days with male count	Fixed	-0.085	0.041	**-2.065**	**0.039**

Stable 14 LMM output of the full models for activity budget changes of parous females in the Suaq population in response to social, ecological and physiological factors (N=221 full day follows of 6 females and 30 FPs). Fixed factors with P<0.05 are indicated in bold. Below the response variable the model comparison is reported based on likelihood ratio tests.

Reponse	Fixed Effects	Type	Estimate	SE	t value	P value
Active hours	Intercept		11.130	0.103		
	z Cumulative female association hours	Fixed	0.061	0.045	1.355	0.177
$\chi^2_{4,13}$=27.47,	z Cumulative male association hours	Fixed	0.034	0.052	0.648	0.518
P=0.001,	Number of copulations	*(Omitted because of collinearity with male-female aggression)*				
ΔAIC=9.47	Male-female cumulative aggression index	Fixed	0.049	0.104	0.473	0.636
	Female-female agonistic interactions (no vs. yes)	Fixed	-0.223	0.600	-0.372	0.710
	z Fruit Availability Index	Control	-0.216	0.070	**-3.103**	**0.004**
	z Age of dependent offspring (y)	Control	0.027	0.078	0.343	0.734
	Social interaction time (h)	Control	0.430	0.338	1.270	0.206
	Consecutive days with female count	Fixed	0.027	0.092	0.293	0.770
	Consecutive days with male count	Fixed	0.076	0.039	1.950	0.052
Feeding hours	Intercept		-4.740	0.434		
	Active time (h)	Offset				
$\chi^2_{5,14}$=19.97,	z Cumulative female association hours	Fixed	0.064	0.054	1.168	0.244
P=0.02,	**z Cumulative male association hours**	Fixed	-0.137	0.065	**-2.105**	**0.036**
ΔAIC =1.97	Number of copulations	Fixed	0.043	0.189	0.225	0.822
	Male-female cumulative aggression index	Fixed	-0.223	0.167	-1.334	0.184
	Female-female agonistic interactions (no vs. yes)	Fixed	0.269	0.727	0.370	0.712
	z Fruit Availability Index	Control	0.248	0.088	**2.812**	**0.009**
	z Age of dependent offspring (y)	Control	-0.110	0.111	-0.990	0.331
	Social interaction time (h)	Control	-0.948	0.420	**-2.257**	**0.025**
	Consecutive days with female count	Fixed	-0.014	0.112	-0.128	0.898
	Consecutive days with male count	Fixed	0.007	0.048	0.149	0.882
Moving hours	Intercept		-9.161	0.108		
	Active time (h)	Offset				
$\chi^2_{5,13}$=24.09,	z Cumulative female association hours	Fixed	-0.067	0.051	-1.320	0.188
P=0.002,	z Cumulative male association hours	Fixed	0.036	0.058	0.624	0.533
ΔAIC=8.09	Number of copulations	*(Omitted because of collinearity with male-female aggression)*				
	Male-female cumulative aggression index	Fixed	-0.160	0.117	-1.374	0.171
	Female-female agonistic interactions (no vs. yes)	Fixed	0.305	0.666	0.458	0.648
	z Fruit Availability Index	Control	0.222	0.063	**3.511**	**0.001**
	z Age of dependent offspring (y)	Control	0.156	0.074	**2.115**	**0.037**
	Social interaction time (h)	Control	-0.170	0.362	-0.469	0.640
	Consecutive days with female count	Fixed	-0.001	0.105	-0.011	0.991
	Consecutive days with male count	Fixed	-0.054	0.043	-1.259	0.209
Resting hours	Intercept		-9.178	0.209		
	Active time (h)	Offset				
$\chi^2_{5,14}$=16.88,	z Cumulative female association hours	Fixed	-0.089	0.059	-1.518	0.131
P=0.05,	z Cumulative male association hours	Fixed	0.060	0.072	0.830	0.408
ΔAIC =1.12	Number of copulations	Fixed	-0.119	0.210	-0.567	0.571
	Male-female cumulative aggression index	Fixed	0.228	0.179	1.278	0.203
	Female-female agonistic interactions (no vs. yes)	Fixed	0.131	0.798	0.164	0.870
	z Fruit Availability Index	Control	0.095	0.160	0.596	0.554
	z Age of dependent offspring (y)	Control	-0.315	0.183	-1.720	0.096
	Social interaction time (h)	Control	-0.457	0.485	-0.943	0.347
	Consecutive days with female count	Fixed	-0.052	0.121	-0.435	0.664
	Consecutive days with male count	Fixed	-0.140	0.054	**-2.577**	**0.011**

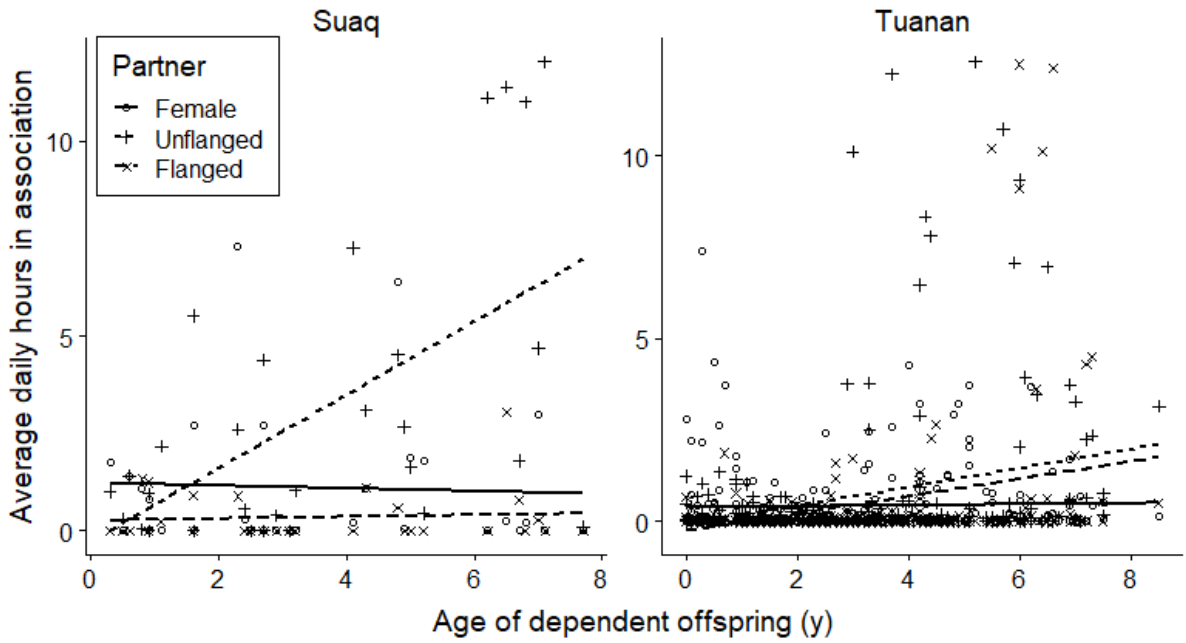


Sfigure 4 Daily feeding, resting and moving hour changes (per active time) (left to right) of parous females in relation to the occurrence of copulations (both forced and voluntary), by study site. The plot is based on the median of the raw data (2095 female full-day focal follows).

Association patterns

Stable 15 LMM output for average daily association hours that parous females spent with a) females, b) unflanged males and c) flanged males depending on study site, FAI, the age of their dependent infant (as proxy for their reproductive state) and number of days available per follow period (FP) (N=280 FP (>4 full-day follows) of 21 parous females (random intercept)).

Response	Fixed effect	Type	Estimate	SE	t value	P value
a) Daily hours with parous females	Intercept		1.249	0.363		
	Site (Suaq vs. Tuanan)	Control	-1.063	0.357	**-2.980**	**0.007**
$\chi^2_{5,7}$=1.03, P=0.60, ΔAIC=2.97	z Fruit Availability Index	Fixed	-0.010	0.062	-0.170	0.865
	z Age of dependent offspring (y)	Fixed	0.065	0.064	1.019	0.309
	Number of days per FP	Control	0.019	0.025	0.782	0.435
b) Daily hours with unflanged males	Intercept		2.432	0.616		
	Site (Suaq vs. Tuanan)	Control	-1.825	0.549	**-3.323**	**0.003**
$\chi^2_{5,7}$=29.123, P<0.0001, ΔAIC=24.43	**z Fruit Availability Index**	Fixed	0.266	0.123	**2.156**	**0.032**
	z Age of dependent offspring (y)	Fixed	0.631	0.126	**4.988**	**<0.001**
	Number of days per FP	Control	0.036	0.050	0.722	0.471
c) Daily hours with flanged males	Intercept		0.624	0.406		
	Site (Suaq vs. Tuanan)	Control	0.228	0.334	0.682	0.499
$\chi^2_{5,7}$=27.35, P<0.0001, ΔAIC=23.28	z Fruit Availability Index	Fixed	0.160	0.089	1.799	0.073
	z Age of dependent offspring (y)	Fixed	0.446	0.090	**4.944**	**<0.001**
	Number of days per FP	Control	-0.049	0.036	-1.365	0.173



Sfigure 5 Average daily hours that parous females spent in association with other parous females, unflanged and flanged males by study site and depending on the age of their dependent offspring (y). Each data point is based on the average of a female follow period, which consists of at least 5 full-day focal follows.

Social interactions during male-female associations

Social interactions among association partners are generally rare in orang-utans compared to other more gregarious primate species. Yet, male-female associations do not only occur when a female is likely fertile (Stable 15; Sfigure 5) and mating only occurred in 11.1% of all male-female associations. To evaluate what other benefits associations could have for either or both females and males, we report the social interactions that were observed during associations including any agonistic or affiliative interaction and sexual investigations.

Affiliative social interactions

Affiliative social interactions, including begging for food, food sharing, social play, and any form of grooming (independent of the directionality) was more likely in associations with unflanged than flanged males (Stable 16). Moreover, affiliative social interactions between males and females increased with the female's offspring age at Suaq, but not at Tuanan (Stable 16; Sfigure 6).

Stable 16 GLMM output for the probability of affiliative social interactions (0/1) in a dyadic association by study site, partner male morph, and the age of the dependent offspring (y) as a proxy of female reproductive state. The association duration (h), taken as all the active time a dyad was <50m, was added as an offset term to correct for the varying time in association ($\chi^2_{3,7}$=20.63, P=0.0004, ΔAIC=12.63, N= 922 associations of 32 parous female IDs and 190 male IDs).

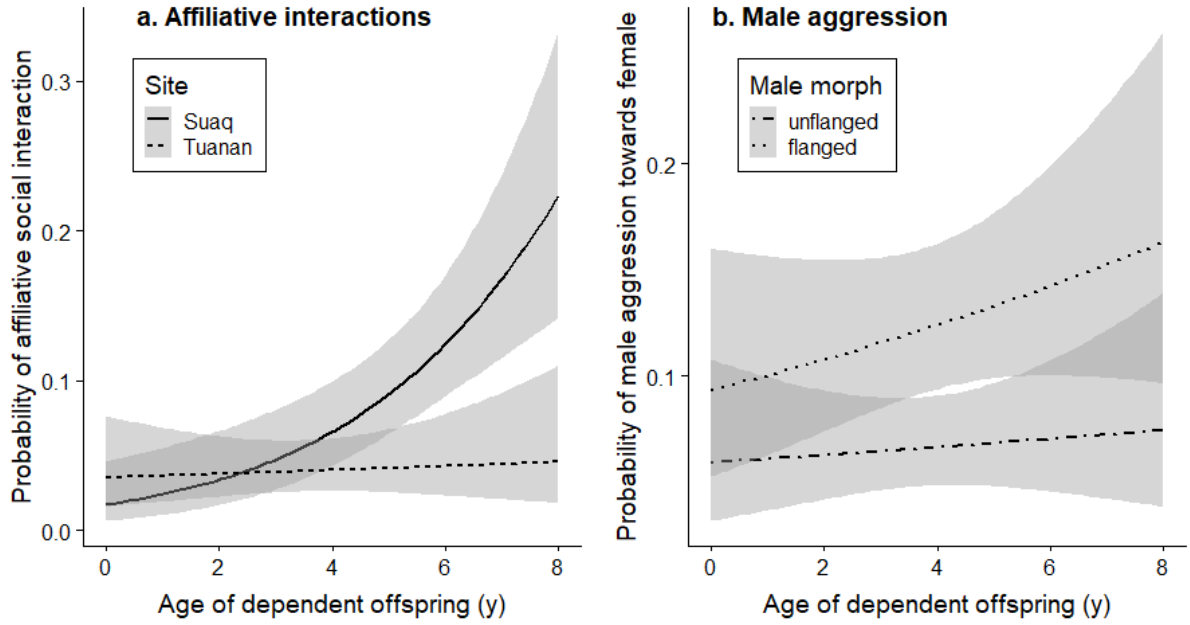
Fixed effects	Estimate	SE	Odd's ratio	z value	P value
Intercept	0.362	0.406			
Association duration	*Offset term*				
Male morph (unflanged vs. flanged)	-1.061	0.472	0.35	**-2.248**	**0.025**
Site (Suaq vs. Tuanan)	-0.541	0.532	0.58	-	-
z Age of dependent offspring (y)	0.907	0.378	2.48	-	-
Site : z Age of dependent offspring (y)	-1.457	0.454	0.23	**-3.211**	**0.001**

Male aggression towards females

Besides the most obvious form of sexual coercion, forced copulation, male aggression towards females in orangutans is rare and especially physical aggression hardly occurs outside of the sexual context. The occurrence of male aggression, including displays, displacement events and chases, was more frequently observed by flanged than unflanged males (Stable 17; Sfigure 6). Moreover, male aggression decreased with the increasing age of the dependent offspring (Stable 17).

Stable 17 GLMM output for the probability of male aggression directed at females (0/1) during dyadic associations by study site, male morph and the age of the dependent offspring as a proxy of female reproductive state. The association duration (h), taken as all the active time a dyad was <50m, was added as an offset term to correct for the varying time in association ($\chi^2_{3,6}$=15.52, P=0.001, ΔAIC=9.52, N= 922 associations of 32 female IDs and 190 male IDs).

Fixed effects	Estimate	SE	Odd's ratio	z value	P value
Intercept	-0.252	0.332			
Association duration (h)	*Offset term*				
Site (Suaq vs. Tuanan)	0.443	0.376	1.56	1.179	0.238
Male morph (unflanged vs. flanged)	1.194	0.346	3.30	**3.450**	**0.001**
z Age of dependent offspring (y)	-0.292	0.142	0.75	**-2.053**	**0.040**



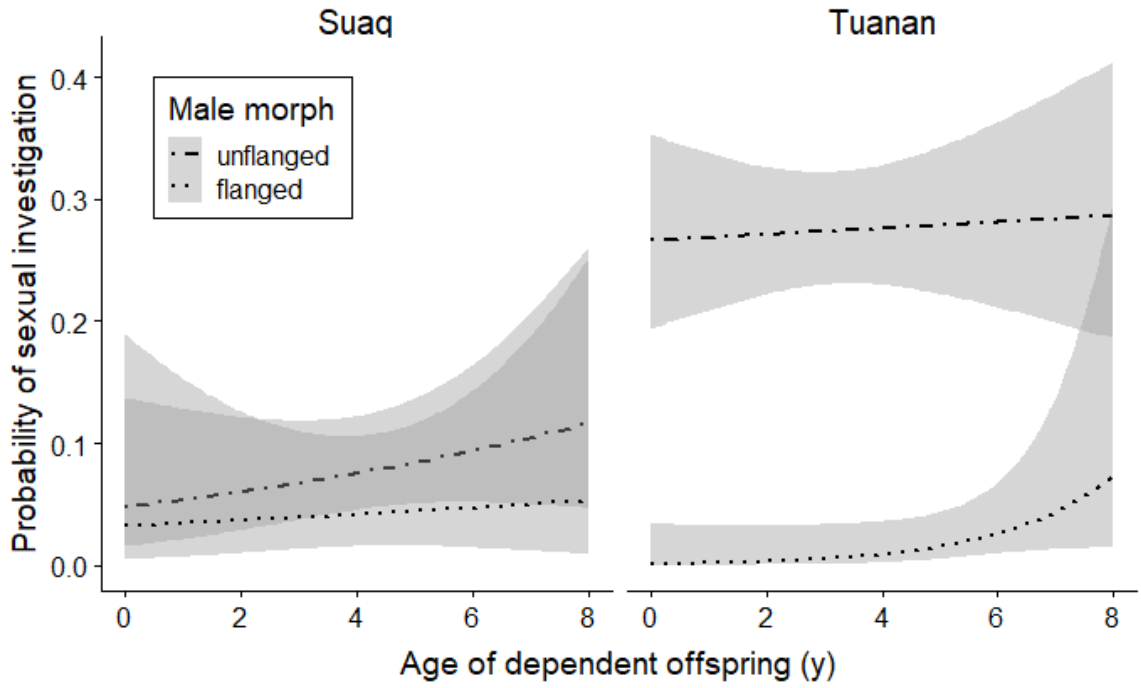
Sfigure 6 Probability of affiliative social interactions (a) and male aggression (b) in a male-female association dyad by the age of the dependent offspring of a female and a) study site and b) male partner morph. The lines indicate the direct relationship between affiliation/aggression probability and the age of the dependent offspring and not the model predictions (Stab. 5 & 6). The data points are based on separate male-female association units (N=922), which may have lasted several days.

Sexual investigations

Males were reported to investigate the genitals of females with hands and mouth and occasionally even drink the females' urine. So far, it is unknown what information the males gain from these sexual investigations. Two scenarios are possible: Males perceive either an olfactory cue indicative of female reproductive state or of previous sexual interactions, i.e. if a competitor had mated previously. Here, we evaluate in which associations these sexual investigations occur. Especially unflanged males at Tuanan investigate females frequently (almost in a third of all associations). Accordingly, the interaction between site and male morph was significant (Stable 18). At Suaq, investigation rates of unflanged and flanged males were in a similar range as that of flanged males at Tuanan (Sfigure 7). Investigations are more likely to occur in longer associations. Moreover, males already investigate the genitals of females with very young dependent offspring and the investigation probability does not change with the infants age. The question then arises how sexual investigations relate to copulations. Copulations did not always occur in associations when sexual investigations took place. Given a sexual investigation was observed, the probability that also a copulation occurred during the same association increased with the age of the dependent offspring (y) and with increasing association duration (Stable 19). The increasing copulations-sexual investigation co-occurrence with the increasing age of the dependent offspring, may be taken as an indication that males perceive some olfactory cue indicative of the female reproductive status. However, future studies including the measurements of female reproductive hormones are needed to investigate what information males gain from the genital investigations.

Stable 18 Binomial GLMM output for the occurrence of sexual investigations during dyadic male-female associations by the study site, male morph, the age of the dependent offspring (y), fruit availability and the number of other males in association ($\chi^2_{3,10}$=135.26, P<0.0001, ΔAIC=121.26, N= 960 associations of 31 female IDs and 174 male IDs).

Fixed effects	Estimate	SE	Odd's ratio	z value	P value
Intercept	-2.996	0.339			
Site (Suaq vs. Tuanan)	1.941	0.350	6.96	-	-
Male morph (unflanged vs. flanged)	-0.590	0.590	0.55	-	-
z Age of dependent offspring (y)	-0.121	0.168	0.89	-0.723	0.469
zFAI	-0.164	0.119	0.85	-1.382	0.167
z Association duration (h)	0.533	0.115	1.70	**4.647**	**<0.001**
Number of other males in association	0.220	0.126	1.25	1.742	0.082
Site * Male morph	-2.784	0.797	0.06	**-3.494**	**<0.001**



Sfigure 7 Probability of sexual investigations by males during dyadic associations with females by the female's dependent offspring age (y), study site (left: Suaq; right: Tuanan) and the male morph (dot-dashed line: unflanged; dotted line: flanged). The lines are based on the logistic correlation between the age of the dependent offspring and the occurrence of sexual investigations and do not depict model predictions.

Stable 19 Binomial GLM output for the probability of copulation occurrence given a sexual investigation was observed during a dyadic association by study site, male morph, age of the dependent offspring, zFAI and association duration (χ^2_5=70.74, P<0.0001, ΔAIC=60.74, N= 122 associations with sexual investigations).

Fixed effects	Estimate	SE	Odd's ratio	z value	P value
Intercept	-3.128	1.095			
Site (Suaq vs. Tuanan)	0.085	0.957	1.09	0.089	0.929
Male morph (unflanged vs. flanged)	1.133	1.099	3.10	1.031	0.302
z Age of dependent offspring (y)	2.346	0.662	10.45	**3.543**	**<0.001**
zFAI	0.213	0.304	1.24	0.700	0.484
z Association duration (h)	1.061	0.309	2.89	**3.435**	**<0.001**

Association maintenance

Stable 20 Binomial GLMM output for the probability that a dyadic association was male-maintained (FHI < 0) by study site, male morph, age of the dependent offspring, copulation occurrence, association duration, overall time spent in the particular dyad and fruit availability ($\chi^2_{3,10}$=59.47, P<0.0001, AIC=510.91, N=435 associations of 26 female IDs and 120 male IDs). *Note*: Without forced copulations, VIFs not at 2 anymore (with forced, then both forced and copulations overall at a VIF=2)

	Estimate	SE	Odd's ratio	z value	P value
Intercept	1.155	0.405			
Site (Suaq vs. Tuanan)	0.108	0.401	1.11	0.270	0.787
Male morph (flanged vs. unflanged)	-0.583	0.303	0.56	-1.927	0.054
z Age of dependent offspring (y)	0.262	0.209	1.30	1.255	0.210
Copulation occurred during association (0/1)	0.090	0.362	1.09	0.249	0.803
z Association duration	1.720	0.406	5.58	**4.234**	**<0.001**
z Overall time spent in dyad	0.249	0.184	1.28	1.355	0.175
z Fruit Availability Index	0.077	0.139	1.08	0.555	0.579

Association maintenance over consecutive days

The survival analysis on the association maintenance over consecutive days was run twice. Once including the associations with unknown start (N=625 associations, reported in the main text) and once excluding them (N=446). The associations with unknown start were included in the analysis, because the start is less likely to be unknown for long associations and by excluding them we would have biased our analysis against such long associations (Stable 21). However, the exclusion of the associations with unknown start does not lead to a different pattern (Stable 22).

Stable 21 Binomial GLMM output for the probability that the start of an association is known depending on study site, association partner sex and the total duration of the association (days) ($\chi^2_{3,6}$=17.26, P=0.0006, N=625 associations of 21 females and 168 different follow periods).

	Estimate	SE	z value	P value
Intercept	1.237	0.342		
Site (Suaq vs. Tuanan)	0.482	0.298	1.618	0.106
Association partner sex (female vs. male)	0.067	0.245	0.273	0.785
Number of days in association	-0.386	0.108	**-3.594**	**<0.001**

Stable 22 Probability of ending an association: Output of the Cox proportional hazard mixed model for the total number of (known) days in association by the type of association partner, study site, age of the dependent offspring (y), and zFAI (χ^2_7=23.47, P=0.001, N=446 associations of which 296 with known end; 20 female identities and 148 FPs).

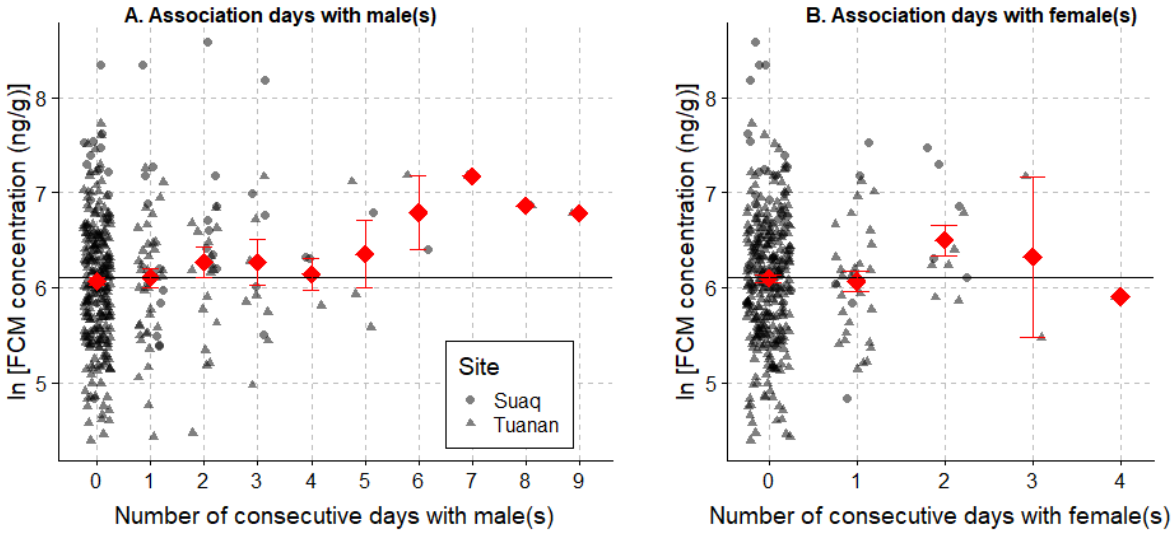
	coef	**SE**	**Hazard ratio**	**z value**	**P value**
Association partner					
Sex (male vs. female)	0.274	0.091	1.315	-	-
Male morph (unflanged vs.flanged)	0.065	0.130	1.067	-	-
Site (Suaq vs. Tuanan)	0.563	0.185	1.756	-	-
Age of dependent offspring (y)	-0.126	0.082	0.882	-1.530	0.130
zFAI	-0.028	0.084	0.972	-0.330	0.740
Association partner sex (male vs. female) : Site	-0.259	0.112	0.772	**-2.300**	**0.021**
Partner male morph (unflanged vs.flanged) : Site	-0.032	0.163	0.968	-0.200	0.840

FCM levels

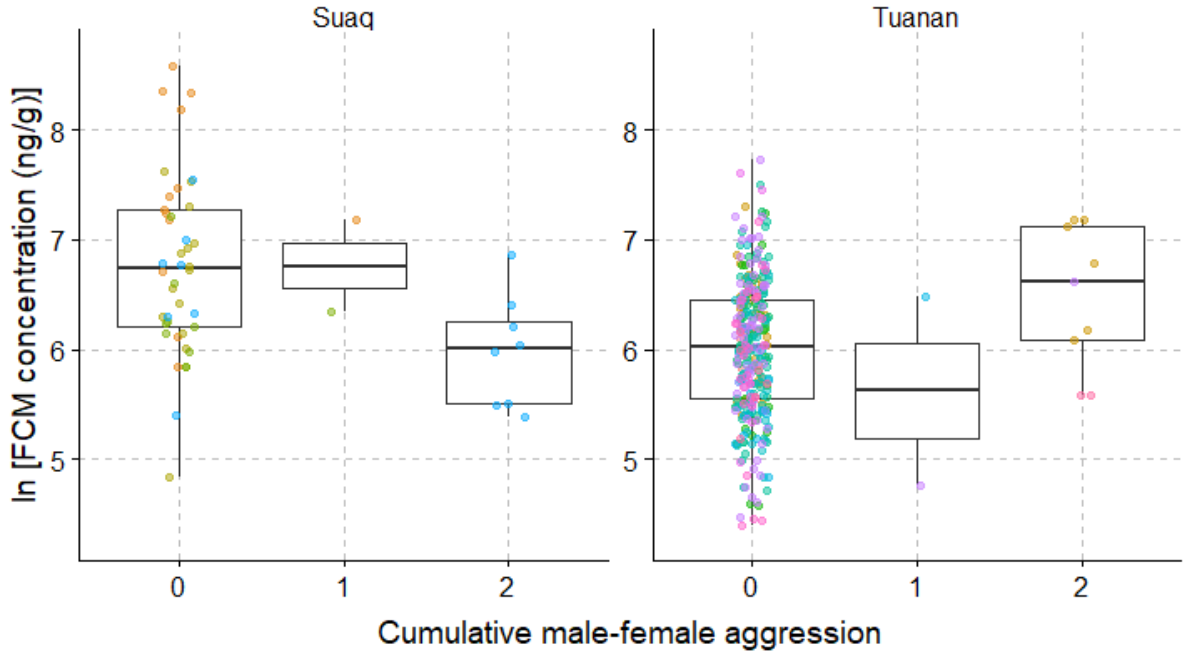
The data set for the FCM levels was limited, especially for the high numbers of consecutive days in associations. Focal animals were normally followed for 5-10 consecutive days and the excretion of cortisol metabolites is delayed for 24-72 hours.

Stable 23 Output of the linear mixed model for the ln-transformed FCM levels (not standardized within individual and method) depending on social factors (consecutive days with males and females, and the occurrence of aggression), population, zFAI, the age of the dependent offspring, daily feeding proportions, the total days followed, the hour of sample collection, the days to sample extraction and the locality of hormone level analysis ($\chi^2_{5,17}$= 21.66, P= 0.03, ΔAIC=2.34; N=370 samples of 96 FPs, 21 IDs and 3 extraction methods).

	Type	**Estimate**	**SE**	**t value**	**P value**
Intercept		6.734	0.331		
Site (Suaq vs. Tuanan)	C	-0.631	0.324	-1.947	0.128
Consecutive days in association with female(s)	F	-0.042	0.052	-0.810	0.418
Consecutive days in association with male(s)	F	0.090	0.031	**2.879**	**0.004**
Male-female cumulative aggression index	F	-0.093	0.071	-1.310	0.191
Female-female agonistic interactions (no vs. yes)	F	-0.008	0.266	-0.030	0.976
Number of days followed	C	-0.004	0.011	-0.335	0.738
z Daily feeding proportion	C	-0.056	0.033	-1.725	0.085
z Age of dependent infant (y)	C	0.008	0.088	0.090	0.929
z Fruit Availability Index	C	0.036	0.048	0.738	0.462
Hour of sample collection	C	-0.003	0.015	-0.178	0.859
z Days to sample extraction	C	0.065	0.055	1.172	0.244
Laboratory (DPZ vs. IPB)	C	0.029	0.152	0.192	0.848



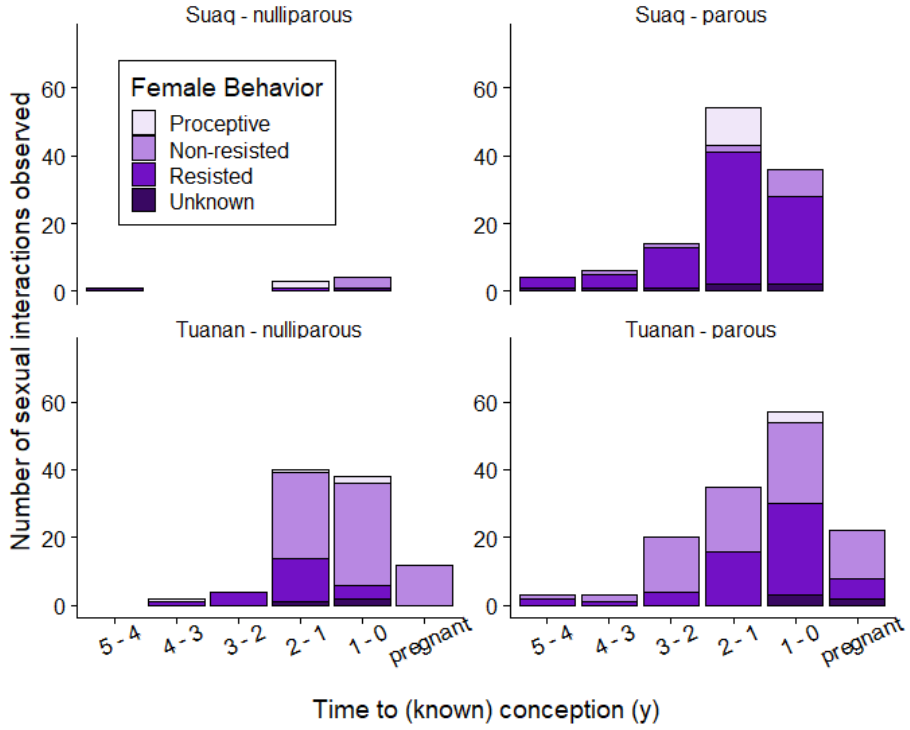
Sfigure 8 FCM levels (ln [FCM concentration (ng/g)]) (y-axis) of parous females in response to consecutive association days with males (A.) and to consecutive association days with females (B). A jitter function was added to the plot to visualize the overlapping data points (consecutive days are only integers). *Note:* The red diamond shaped points indicate the mean FCM levels with the error bar in red. The black line indicates the overall mean of all available female FCM levels which were included in the analyses.



Sfigure 9 Female FCM levels (ln [FCM concentration (ng/g)]) in relation to cumulative male aggression (0=no aggression, 1=short, non-physical aggression (not in the direct sexual context), 2=forced copulation or other form of sexual coercion) by study population. Different individuals are indicated in different color.

Chapter 4: Female Mating Patterns

Observed sexual interactions during the study period



Sfigure 10 Increase of sexual interactions as conception approaches: Bar plot of all observed sexual interactions depending on the females' behaviour (legend) by the study site (top: Suaq; bottom: Tuanan) and female parity (left: nulliparous; right: parous). Note: The x-axis shows the years to conception. The date of conception was inferred from the birth date of the offspring as indicated in Table 8. (Note: This figure also includes failed attempts; the absence of pregnancy mating at Suaq can be explained by a lack of observation time on pregnant females (Figure 14); also see Fox [1998])

Stable 24 Overview for all sexual interactions observed during the study period depending on interaction type, female parity and male morph and by study site (N=511 sexual interactions with known female behaviour). Note: Sexual interactions for which it was unknown if intromission was achieved or the female's behaviour was not described were excluded from this overview. The overview includes only the counts of the sexual interactions involving females for which conception was known or could be estimated. In brackets, the total number of observed sexual interactions also involving females for which the timing of conception was unknown is indicated.

		Study site	**Suaq** *N=113 (173)*		**Tuanan** *N=228 (338)*	
Sexual interaction		**Parity** / **Morph**	**Nulliparous** 2 females *(5)*	**Parous** 4 females *(8)*	**Nulliparous** 4 females *(10)*	**Parous** 10 females *(17)*
Copulations	Resisted copulation	unflanged	1 (1)	75 (95)	17 (30)	36 (56)
		flanged	0 (1)	1 (2)	0 (0)	6 (11)
	Not resisted copulation	unflanged	0 (1)	12 (20)	61 (88)	65 (78)
		flanged	3 (8)	0 (0)	6 (7)	11 (23)
	Proceptive copulation	unflanged	0 (0)	0 (2)	3 (4)	1 (1)
		flanged	2 (10)	4 (4)	0 (0)	2 (4)
Attempt	Resisted attempt	unflanged	0 (0)	7 (14)	5 (10)	13 (18)
		flanged	0 (0)	1 (1)	0 (0)	1 (2)
	Proceptive attempt	unflanged	0 (0)	0 (0)	0 (0)	0 (0)
		flanged	0 (0)	7 (7)	1 (1)	0 (0)

Stable 25 Sexual interaction initiations (of body contact) by female parity, male morph and study site.

		Unflanged males			Flanged males		
Initiation of body contact by		Female	Male	Both	Female	Male	Both
Suaq	Nulliparous females	0	1	0	6	9	0
	Parous females	1	127	0	10	3	0
Tuanan	Nulliparous females	2	73	2	1	0	0
	Parous females	1	91	3	4	23	0

Number of mating partners and copulations per conception

Overall the period prior and post conception, as reported in the main text

Stable 26 Poisson GLMM output for a) the number of mating partners per conception and b) the number of copulations observed per conception per female (N=21 conceptions of 13 different female IDs). Female identity was set as a random intercept and the active time a female was observed as an offset term to correct for the observation bias.

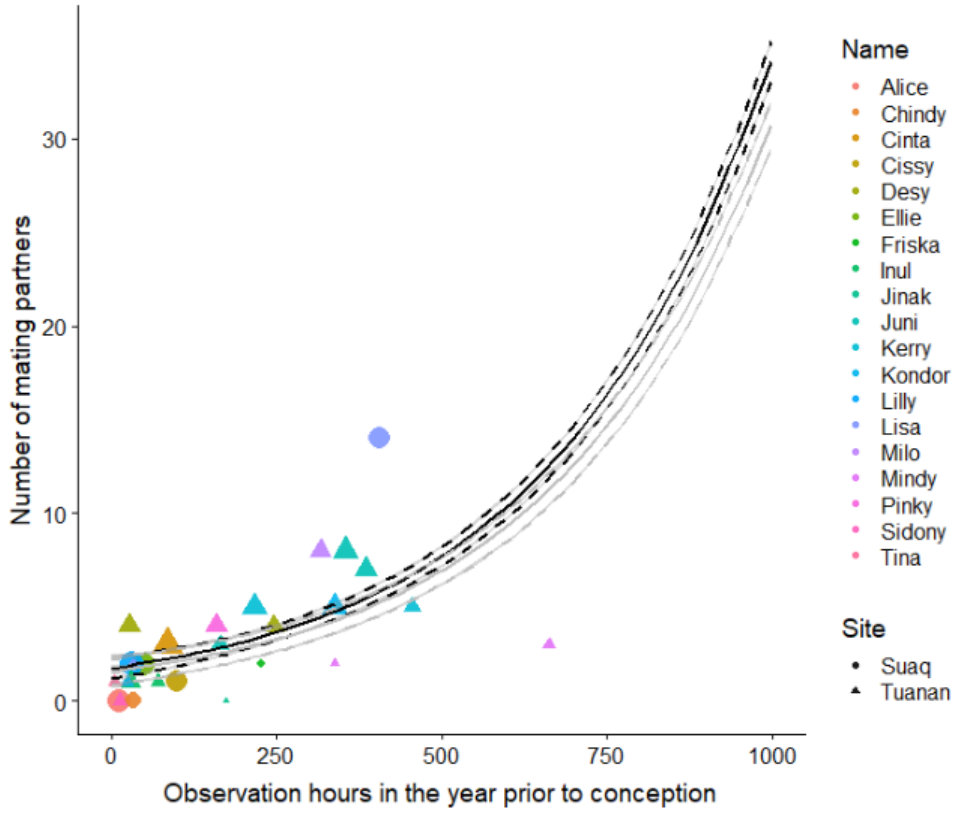
Response	**Fixed effects**	**Estimate**	**SE**	**z value**	**P value**
Number of mating partners	Intercept	-7.153	0.630		
	Observation hours	*Offset*			
	Site (Suaq vs. Tuanan)	0.389	0.437	0.892	0.373
$\chi^2_{2,5}$=14.84, P=0.002	Female Parity (nulliparous vs. parous)	0.112	0.309	0.362	0.717
	Proportion of observation time with males	3.247	0.742	**4.375**	**<0.001**
Number of copulations	Intercept	-6.915	0.529		
	Observation hours	*Offset*			
	Site (Suaq vs. Tuanan)	1.500	0.499	3.005	0.003
$\chi^2_{2,7}$=66.9, P<0.0001,	Female Parity (nulliparous vs. parous)	1.388	0.520	2.668	0.008
$\chi^2_{2,7}$=12.99, P=0.0003	Number of mating partners	0.027	0.023	1.192	0.233
	Proportion of observation time with males	3.565	0.562	**6.344**	**<0.001**
	Site * Female Parity	-2.136	0.579	**-3.691**	**<0.001**

Number of mating partners and copulations in the year prior to conception

Sexual interactions increase as conception approaches. As an attempt to estimate how many mating partners females actually have on average per conception, we extrapolated the model fit for the number of observed mating partners by individual females, taking into account study site, female parity, the proportion of observation time in association with males and the actual observation hours available (Sfigure 11). Note that the model predictions do not take male availability (i.e. number of males present in this year) or any measures of male-male competition or female choice for certain males into account, which all may reduce mating partner number.

Stable 27 Poisson GLMM output for the number of mating partners and copulations in the year preceding conception by study site, female parity and observation time per female (N=23 conceptions of 15 females). For the number of mating partners the proportion of time spent in association was added as a fixed effect, whereas there were collinearity issues with the number of males in the number of copulations analysis

Response	Fixed effects	Estimate	SE	z value	P value
Number of mating partners	Intercept	0.529	0.493		
	Site (Suaq vs. Tuanan)	0.106	0.319	0.332	0.740
$\chi^2_{2,6}$=23.06, P=0.0001	Parity (nulliparous vs. parous)	0.030	0.273	0.109	0.913
	Proportion in association with males	1.360	0.497	**2.738**	**0.006**
	z Observation time (h)	0.775	0.182	**4.265**	**<0.001**
Number of copulations	Intercept	1.353	0.362		
	Site (Suaq vs. Tuanan)	0.195	0.292	0.666	0.506
$\chi^2_{2,6}$=136.01, P<0.0001	**Parity (nulliparous vs. parous)**	-0.748	0.202	**-3.696**	**<0.001**
	Number of mating partners	0.228	0.036	**6.373**	**<0.001**
	z Observation time (h)	0.330	0.200	1.650	0.099



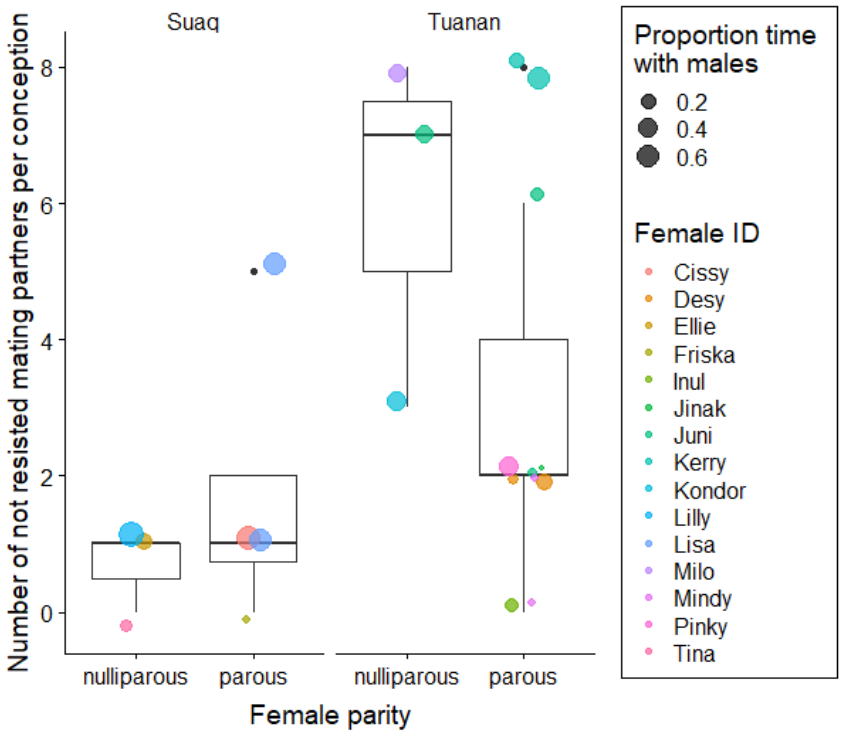
Sfigure 11 Model predictions for the number of mating partners by female observation hours: the black lines show the predictions (and 95% confidence intervals as dashed lines) for the Tuanan population, the grey lines the Suaq population. The data points indicate actual mating partner numbers (y-axis) for individual females (in different colours) in their year immediately preceding (known) conception by the available observation hours (x-axis). The size of the data points is relative to the proportion of observation hours a female spent in association with males. As a full-day female focal follow lasted on average 10.94±SD 0.16 hours, 1000 observation hours correspond to about 90 observation days

Number of non-resisted mating partners

Because sexual interactions are mostly male-initiated, the polyandrous mating pattern seen in orang-utans may be labelled as an artefact of the frequent sexual coercion by males, and thus, convenience polyandry. However, even the number of non-resisted sexual interactions is well above one (at least for Tuanan where more data is available) (Sfigure 12).

Stable 28 Poisson model output for i) the number of non-resisted mating partners (at least 1 copulation without resistance) (GLM) and ii) the number of non-resisted copulations per conception (Poisson GLMM) by study site, female parity and the proportion of (observation) time in association with males (N=21 conceptions of 15 females). (Note: We could not account for female identity in the mating partner number model due to singularity issues)

Response	Fixed effects	Estimate	SE	z value	P value
Number of non-resisted mating partners	Intercept	-7.658	0.597	-12.835	<0.001
	Observation time (h)	*Offset*			
χ^2_3=27.15, P<0.0001	Site (Suaq vs. Tuanan)	0.738	0.412	1.791	0.073
	Female parity (nulliparous vs. parous)	-0.198	0.282	-0.704	0.482
N=21 conceptions	**Proportion of observation time with males**	3.588	0.750	**4.786**	**<0.001**
Number of non-resisted copulations	Intercept	-6.537	0.512	-12.762	<0.001
	Observation time (h)	*Offset*			
$\chi^2_{2,5}$=55.93, P<0.0001,	Female identity (N=15)	*Random intercept*			
	Site (Suaq vs. Tuanan)	0.799	0.399	**2.001**	**0.045**
	Female parity (nulliparous vs. parous)	-0.898	0.273	**-3.293**	**0.001**
	Proportion of observation time with males	3.790	0.685	**5.531**	**0.000**



Sfigure 12 Number of non-resisted mating partners per conception by female parity (x-axis) and separated by study site (left: Suaq; right: Tuanan). Data point size is relative to the proportion of time a female spent in association with males per total observation time. Female identity is shown in colour.

Stable 29 Successful female resistance (no intromission achieved) given that there was a male-initiated and female resisted sexual interaction: Output of the binomial GLMM ($\chi^2_{2,6}$ = 0.74, P=0.94, N=141 resisted sexual interactions of 15 different females)

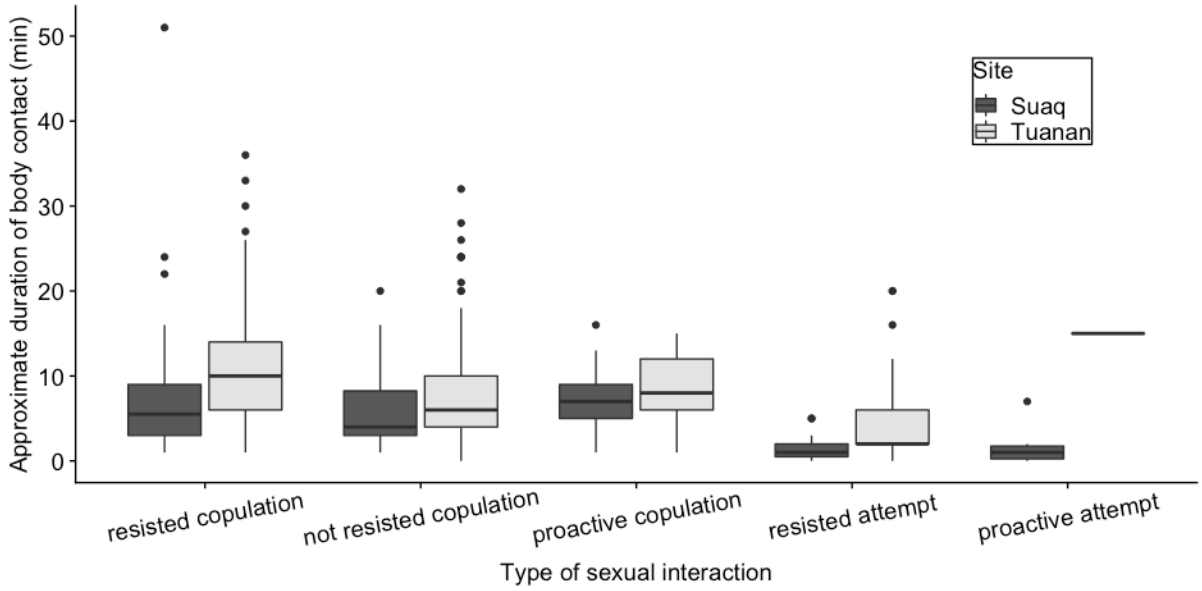
	Estimate	SE	Odd's ratio	z value	P value
Intercept	-1.391	0.945			
Male morph (flanged vs. unflanged)	0.631	0.992	1.88	0.636	0.525
Time to (known) conception (y)	0.115	0.252	1.12	0.455	0.649
Female parity (nulliparous vs. parous)	0.158	1.035	1.17	0.153	0.878
Interruption by another male (no vs. yes)	-0.061	0.826	0.94	-0.074	0.941

Details on duration of sexual interactions

Failed attempts, both male initiated, i.e. resisted attempts, and female initiated, i.e. proceptive attempts, were characterized by shorter body contact than copulations (β=0.217±0.029, t=7.424, P<0.001). Overall, the type of sexual interaction did improve the model fit significantly for the duration of body contact ($\chi^2_{8,12}$=93.18, P<0.0001, ΔAIC=85.2).

Stable 30 Body contact duration during sexual interactions: LMM output for the ln-transformed duration of body contact (minutes) during a sexual interaction (N=485 sexual interactions, of 273 different dyadic associations 88 males and 36 females) ($\chi^2_{5,12}$=96.66, P<0.0001, ΔAIC=82.7).

		Estimate	SE	t value	P value
Intercept		1.444	0.148		
Type of sexual interaction	**Attempt vs. copulation**	0.217	0.029	**7.424**	**<0.001**
	Resisted attempt vs. proceptive attempt	-0.235	0.152	-1.547	0.123
	Proceptive copulation vs. other copulations	-0.003	0.050	-0.067	0.947
	Resisted copulation vs. not resisted copulation	-0.111	0.036	**-3.054**	**0.002**
Site	Suaq vs. Tuanan	0.221	0.119	1.865	0.071
Female parity	nulliparous vs. parous	0.055	0.096	0.575	0.567
Male morph	flanged vs. unflanged	0.026	0.105	0.244	0.807



Sfigure 13 Duration of body contact (min) between male and female during sexual interactions depending on the type (x-axis) and the study site (red: Suaq; blue: Tuanan).

Details on female proceptive behaviour

At Suaq, a parous female (Dodi) was observed during two consecutive days to repeatedly (7x) approach Islo, the dominant flanged male, and handle his genitals with her hands and mouth and proceptively positioning herself for mating in vain (Sfigure 10). During these 2 days no copulation was observed between Dodi and Islo. Dodi only conceived approximately 1 year after these interactions were observed. At Tuanan, failed proceptive attempts were observed twice from nulliparous females towards flanged males. One was towards a flanged male who had just won a physical fight against another flanged male. The female without any dependent offspring approached the male and tried to involve him in mating without success. The female was not known to observers and the time of conception remains unknown. The second incidence was a nulliparous female 1.5 year prior to her first conception.

Chapter 4: Faecal Progesterone Metabolite Levels

additionally with Taufiq Purna Nugraha[4,5], Neneng Mardianah[2], Manuela Townsend[1], Muhammad Agil[5], Michael Heistermann[6]

1) Department of Anthropology, University of Zurich, Switzerland
2) Universitas Nasional, Jakarta, Indonesia
4) Research Center for Biology, Indonesian Institute of Sciences (LIPI), Cibinong, Indonesia
5) Agricultural University Bogor, IPB, Indonesia
6) Endocrinology Laboratory, German Primate Center, Leibniz-Institute for Primate Research, Germany

Methods

Sample collection and hormone measurement

Faecal hormone samples of focal individuals were collected non-invasively upon spontaneous defecation to measure progesterone metabolites levels (pregnanediol-glucuronide) (fPdG) (for details also see chapter 3). Because of logistic limitations, different sample preservation methods had to be used depending on the availability of reliable electricity supply. Faecal samples (2-5 g) were either frozen at -18˚C degrees upon return to the field station in the evening ("frozen") or kept in 4ml 80% ethanol immediately upon collection of the sample ("alcohol" samples). Sample extractions were performed either by a lyophilisation process in the laboratory ("frozen") or using the field extraction method ("alcohol") as validated and described in detail by Nugraha et al. (2016). We analysed fPdG levels using enzyme immunoassays (EIA) as described and designed by Heistermann and Hodges (1995), and previously validated for orang-utans (Weingrill et al., 2011). The faecal samples were analysed in three different cohorts at the hormone laboratories of the German Primate Center, Göttingen (DPZ) (N=59 samples) and the University of Agriculture, Bogor (IPB) (N=315 samples). Location of the laboratory was accounted for in the statistical analyses (see below). At both laboratories intra-assay CV values were below 10% and inter-assay CVs below 15%. All fPdG concentrations were expressed in ng/g dry faecal weight.

Statistical analysis

Despite the long-term collection effort of faecal samples, we had only patchy records on hormone levels of individual females and could not directly assess cycling activity over several weeks or months from repeated, daily faecal samples. Orang-utans are solitary and focal animals are usually not followed more than 10 days in a row (and thus samples collected), with a break of at least 5 weeks between the follow periods, to avoid over-habituation and reduce the animals' exposure to human observers. Progesterone levels rise 2-3 days after ovulation to more than 2 standard deviations above the baseline level and remain high throughout the luteal phase (Heistermann et al., 1995). Because of our limited data set, we conducted two different approximate analyses. First, we compared average fPdG levels of females in different phases (non-sexually active, sexually active and pregnant, see below). Second, we conducted permutation tests with the data from the pilot study (captivity) as expected data distribution for sexually active females who would be expected to exhibit ovulatory cycles (section "Comparison to female uPdG level variability in captivity"). Third, we linked the endocrine data to behavioural data (last section).

fPdG levels of females in different reproductive phases

Methods

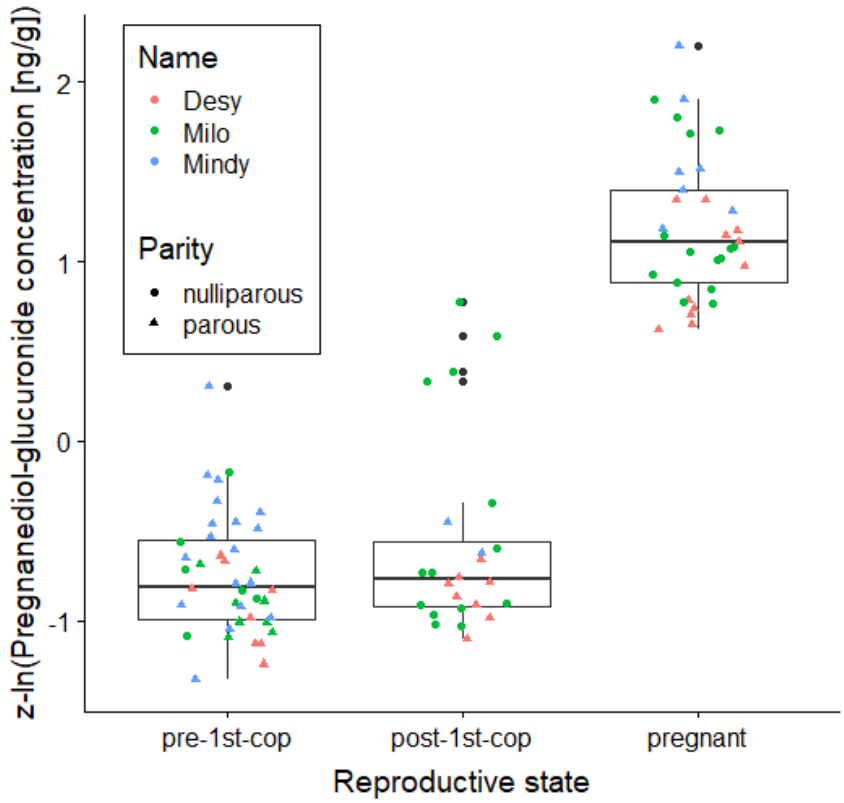
To analyse the hormone levels, we set up 3 categories for the female reproductive state: 1) prior to the first copulation observation ("pre-1st-cop") (parous females: starting from the birth of the dependent infant; nulliparous females: starting with their independent ranging from their mothers [Ashbury et al. in rev.; van Noordwijk et al. 2009]), 2) after the first copulation was observed ("post-1st-cop") and 3) pregnant. First, we analysed the data set containing all morning samples available of females, for whom at least 8 samples of 2 reproductive states were available. Hence, we assessed cross-sectional hormone levels, which is not ideal. Second, we took a more conservative data subset composed of 3 individual females from the Tuanan population for whom samples for each reproductive state (lactating/acyclic [pre-1st-cop], sexually attractive [post-1st-cop], pregnant) were available. We conducted linear mixed models (LMM) including the female identity as a random intercept. In order to normalize the residual distribution, fPdG levels were ln-transformed prior to the analyses (ln-fPdG). The control models contained the time to sample extraction, female parity and local FAI as control factors. For the longitudinal (within-individual) analysis, we z-transformed the ln-fPdG values within each individual female and method of extraction, to assess the variability of fPdG levels within each individual rather than between individuals or methods (van de Pol and Wright, 2009). Additionally, we added the analyses batches as control factor to the longitudinal model. No z-transformations were done in the cross-sectional dataset, because we did not have fPdG levels for all reproductive states for all the females. Therefore, we included the extraction method as a fixed factor in the model to control for biases introduced by different extraction methods. However, the laboratory session could not be added in the cross-sectional analysis, because the extraction method used correlated with the laboratory session (VIF>2). The control models were significantly better than the null model (with the random intercept only) for both the longitudinal dataset ($\chi^2_{3,8}$=29.4, P<0.0001, ΔAIC=19.4) and the cross-sectional model ($\chi^2_{3,9}$=13.9, P=0.03, ΔAIC=1.9). Female reproductive state was added as the only fixed factor in the full models. We set contrasts to compare fPdG levels first between not pregnant and pregnant and subsequently between pre-1st-cop and post-1st-cop periods.

Results

Within individuals, fPdG levels were significantly elevated during pregnancy (β=0.687±0.036, t=19.13, P<0.001), as expected. However, we could not find any evidence for higher fPdG values, indicative of ovarian activity, of sexually active females (*"post-1st-cop"*) compared to non-sexually active females (*"pre-1st-cop"*) (β=0.065±0.057, t=1.143, ns.) (Stable 31, Sfigure 14).

Stable 31 Faecal pregnanediol-glucuronide concentration (ng/g) within female longitudinal analyses: LMM output for within individual z-transformed ln-fPdG concentration changes with reproductive state as a proxy for female cycling activity. Restricted dataset of only 3 females for which samples for each reproductive state (Pre-1st-Cop = prior to observation of first copulation; Post-1st-Cop = after the observation of the first copulation; Pregnant) were available ($\chi^2_{8,10}$=155.91, P<0.0001, pseudo-R^2=0.88, N=96 morning samples of 3 females). Note: The "Type" column indicates, if the factor was entered as fixed or control factor.

	Type	Estimate	SE	t value	P value
Intercept		0.137	0.212		
Female Reproductive State	Fixed				
not pregnant vs. pregnant		0.687	0.036	**19.131**	**<0.001**
Pre-1st-Cop vs. Post-1st-Cop		0.065	0.057	1.143	0.256
Female parity (nulliparous vs. parous)	Control	-0.156	0.172	-0.904	0.371
zFAI	Control	0.179	0.059	**3.036**	**0.003**
Sample batch	Control				
DPZ vs. IPB1		-0.226	0.170	-1.332	0.186
DPZ vs. IPB2		0.077	0.177	0.435	0.664
Delay to extraction (days)	Control	0.000	0.000	-0.224	0.824



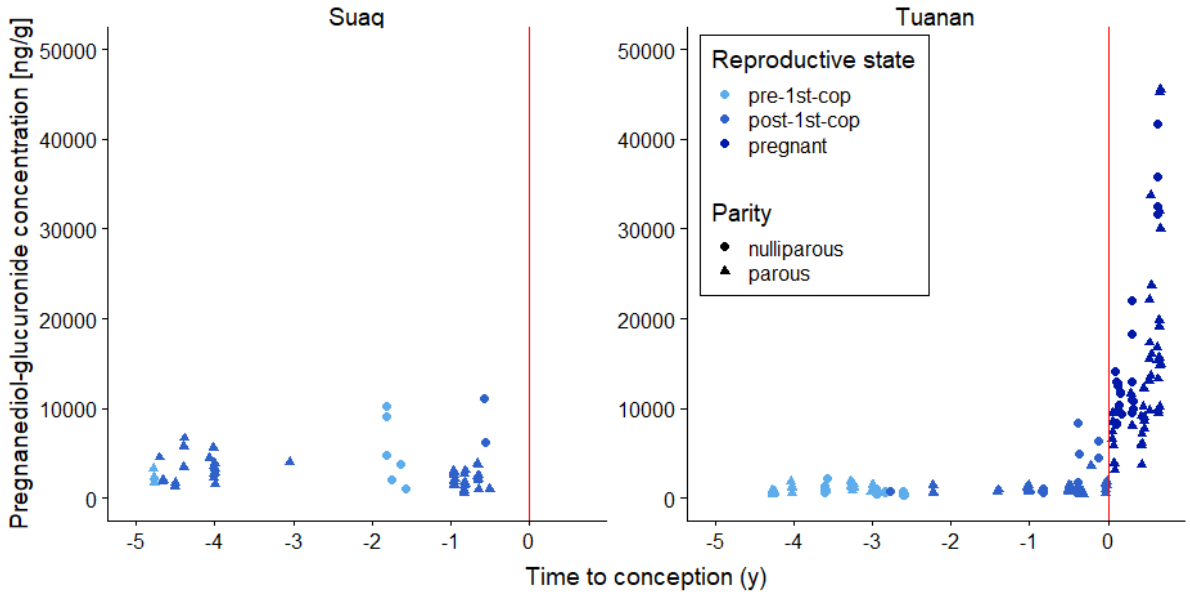
Sfigure 14 Faecal pregnanediol-glucuronide (fPdG) concentration (ng/g) depending on the female reproductive state and by female identity. PdG concentrations are shown as ln-transformed values and are standardized (scaled) within individual.

The cross-sectional analysis of fPdG values including all females confirmed the higher fPdG levels of pregnant than not pregnant females (β=0.916±0.027, t=34.46, P<0.001). Moreover, sexually active (*post-1st-cop*) females tended to have higher fPdG concentrations than non-sexually active females (β=0.071±0.038, t=1.858, P=0.06) (Stable 32). This difference was driven by one nulliparous female (Milo) (Sfigure 14). When excluding Milo from the analyses, there was no difference in fPdG levels between non-sexually active (*pre-1st-cop*) and sexually active (*post-1st-cop*) stage (β=0.004±0.004, t=0.985, ns.). Further, when only taking fPdG levels of females who were not pregnant

into account, the model fit did not improve when adding the time to conception as a fixed, linear effect ($\chi^2_{9,10}$=1.56, ns., ΔAIC=0.4, N=180 of 9 different females) (Sfigure 15), indicating that average fPdG levels did not rise as conception approached and as the frequency of sexual interactions increased. Yet, at least one female (Milo) exhibited higher fPdG values 3 months prior to the known conception of her first infant (Sfigure 14, Sfigure 15), indicating either cycling activity (i.e. elevated fPdG levels during the luteal phase) or a failed pregnancy.

Stable 32 Faecal pregnanediol-glucuronide concentration (ng/g) changes cross-sectional analyses: LMM output with reproductive state as fixed effect, controlling for study site, female parity status, zFAI, Number of samples available, the extraction method used and the delay to sample extraction. LMM output including females for which at least 8 morning samples with fPdG levels for at least 2 reproductive states were available ($\chi^2_{9,11}$=540.05, P<0.0001, N=373 of 12 different females). Note: The "Type" column indicates, if the factor was entered as fixed or control factor.

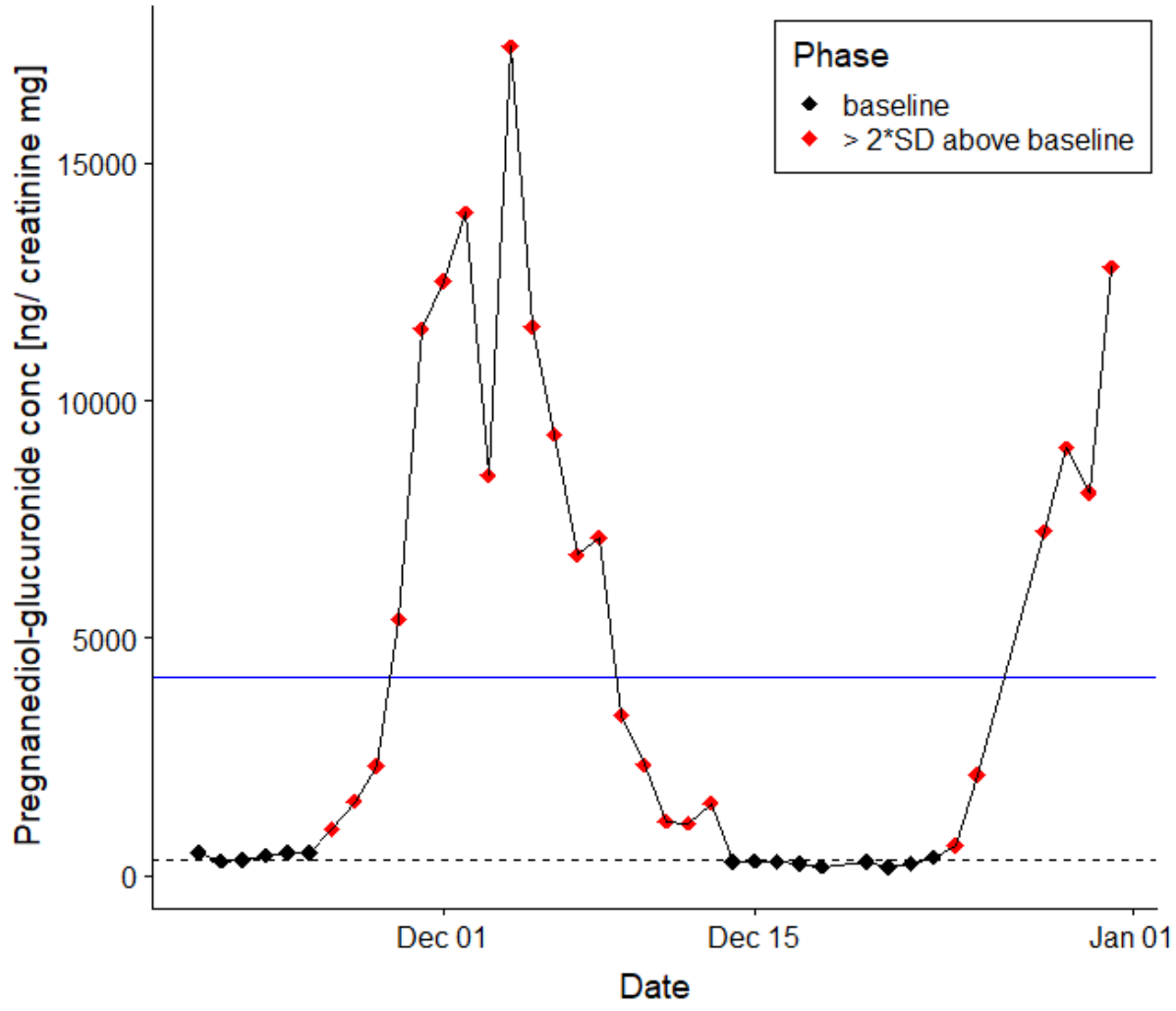
	Type	Estimate	SE	t value	P value
Intercept		8.986	0.227		
Female Reproductive State	Fixed				
not pregnant vs. pregnant		0.916	0.027	**34.456**	**<0.001**
Pre-1st-Cop vs. Post-1st-Cop		0.071	0.038	1.858	0.064
Site (Suaq vs. Tuanan)	Control	-0.973	0.193	**-5.051**	**<0.001**
Female parity (nulliparous vs. parous)	Control	-0.219	0.109	**-2.016**	**0.045**
zFAI	Control	0.000	0.028	0.001	0.999
Number of samples per female	Control	-0.011	0.006	-1.967	0.071
Delay to extraction (d)	Control	0.000	0.000	**3.974**	**<0.001**
Extraction method (alcohol vs. frozen)	Control	0.074	0.137	0.544	0.587



Sfigure 15 Faecal pregnanediol-glucuronide (fPdG) concentrations (ng/g) depending on the time to conception (y), if the first copulation was observed (colour), and the female parity (shape of data points). The red vertical line indicates the (estimated) timing of conception. (Note: different extraction methods were used at Suaq (left) and Tuanan (right), therefore values cannot be directly compared between the two sites).

Comparison to female PdG level variability in captivity

We collected urine samples from a nulliparous female in the Basel Zoo during 41 days (November and December 2015) to measure urinary progesterone metabolite levels and assess ovarian activity. The hormone analyses were conducted at DPZ, Göttingen, using enzyme immunoassays according to an established and validated protocol (DPZ protocol). We found evidence for two ovulations during this period and a clear distinction between the uPdG levels of the follicular (black points in Sfigure 16) and the luteal phase (red points). The time span between the two raises of uPdG was 28 days (26 November to 24 December) and during this period uPdG values were two standard deviations above the baseline uPdG levels during 18 days (Sfigure 16).

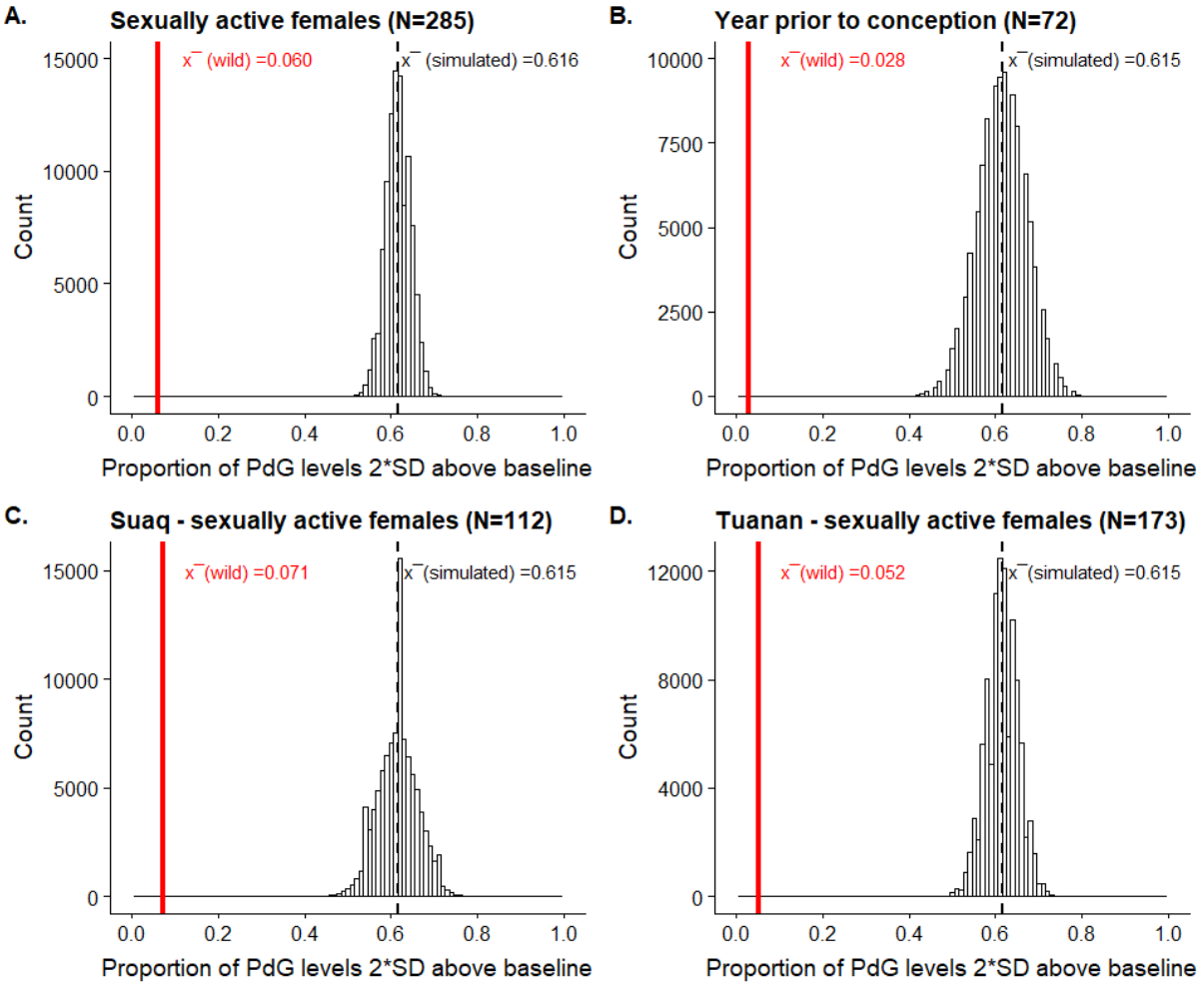


Sfigure 16 Urinary Pregnanediol-glucuronide concentration (ng/mg creatinine) (uPdG) of a nulliparous female from the Basel Zoo (N=39 days) illustrating evidence for two ovulations. The blue line shows the average uPdG level over the entire period.

Based on the likelihood of these uPdG levels being two standard deviations above baseline, we simulated 10 000 random data sets with an expected ratio of uPdG levels above baseline. Subsequently, we compared the expected simulated data sets based on the captivity data to the observed proportion of fPdG levels above baseline in the wild. From our fPdG data at Tuanan and Suaq, we evaluated the subset of females that were known to be in the sexually active period (*"post-1st-cop"*) and before known conception. We evaluated on the individual and method level, if a female exhibited fPdG levels which exceeded her other values by 2 standard deviations. Such a procedure is sample size dependent. Because

for some females the sample size was very small and sample collection spread over several years, we cannot exclude that our small sample sizes have an effect on the estimated baseline fPdG level and the probability of finding values exceeding two standard deviations. These analyses are therefore to be treated with caution and are merely presented to generate new hypothesis on the orang-utan female reproductive physiology.

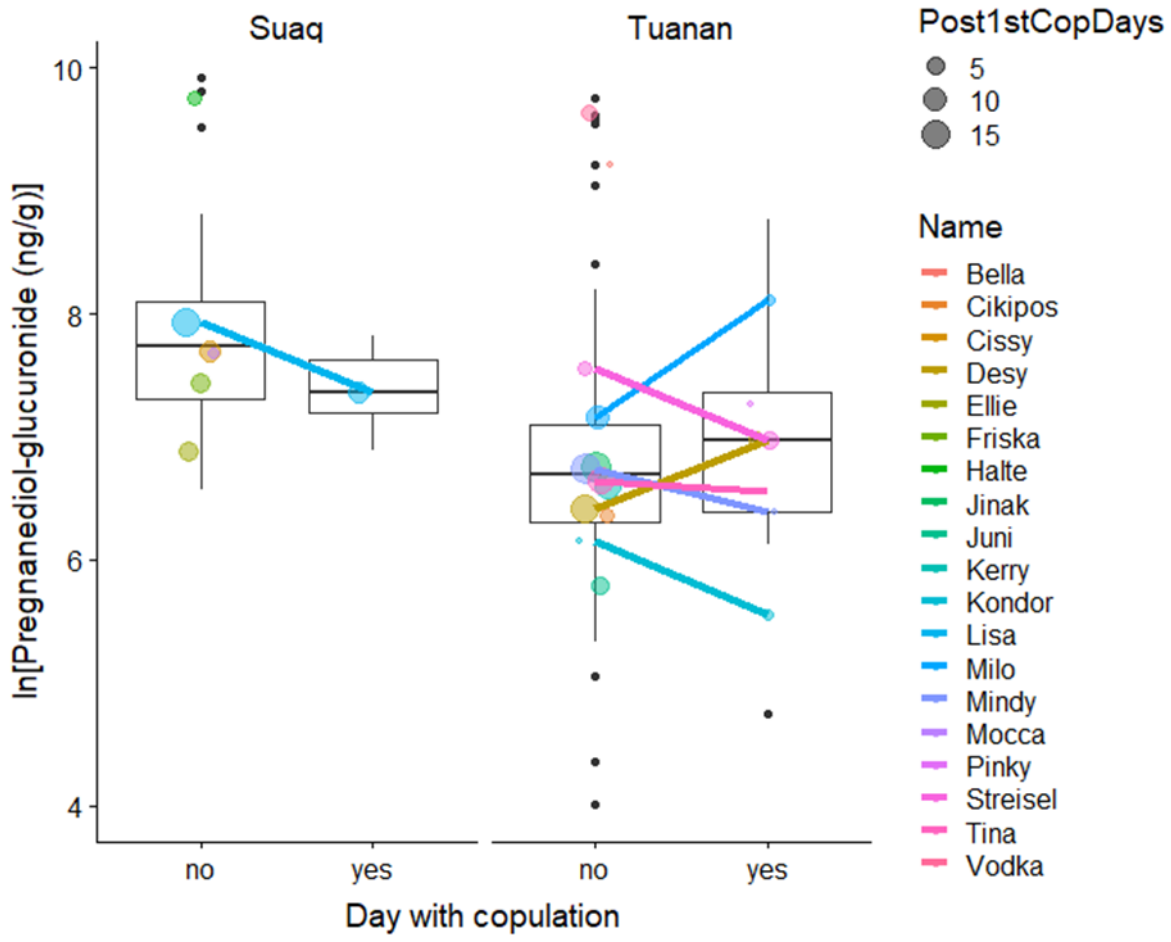
The observed frequency of elevated fPdG levels in sexually active females was far below the expected distribution based on the ovarian cycle from the captive female (Sfigure 17). Also when only taking the samples from females one year prior to conception, the frequency of observed elevated fPdG levels was far below the expected distribution based on the ovarian profile from captivity.



Sfigure 17 Histogram of the mean probability that uPdG levels exceed the baseline by 2*sd (standard deviation) for each simulated data set (10 000 iterations) based on the ovarian cycle of the captive orang-utan female (Sfigure 16) by A. all sexually active females (N=285) ("post-1st-cop", i.e. females that were observed to copulate any time prior to sample collection), B. all sexually active females for which samples of the year preceding known conception (N=72 samples), C. all sexually active females at Suaq, D. all sexually active females at Tuanan. *Note:* The red line indicates the mean proportion of samples from the wild population which exceeded the individual fPdG baseline level by 2*SD or more.

Progesterone metabolite levels and sexual behaviour

Steroid hormones are only excreted in the faeces after a time lag of 48-72 hours (Weingrill et al., 2011). In order to relate fPdG levels to the observed sexual behaviour, hormone levels had to be related to the behaviour observed 3 days before sample collection (given that it was a first morning sample) (for details see chapter 3). For a small subset of the hormone levels, sexual interactions were observed on these reference days (Sfigure 18). If males would copulate with females that are likely to ovulate, fPdG values would be expected to be low, given that progesterone levels only raise after ovulation. In Sfigure 18, no such pattern can be seen. We hypothesize therefore that males do not have cues of female hormonal status, despite their regularly observed investigations of females' genitals. This goes in accordance with previous captive study findings (Nadler, 1981). However, our sample size is extremely small and it presents a starting point to further evaluate the reproductive physiology of female orang-utans.



Sfigure 18 ln-transformed faecal pregnanediol-glucuronide (fPdG) levels (ng/g) on days with and without copulations divided by study site (left: Suaq; right: Tuanan) and by individual females (Suaq: N=6; Tuanan: N=13), who have been observed to be sexually active ("post-1st-cop" category). The boxplots are based on the median of daily PdG levels (only morning samples). The coloured points stand for the average of individual female and category (no/yes copulation) and the lines connect the within-female averages of days with and without copulations. The size of the data points is relative to the number of days included in the average for each female and category.

Discussion

Orang-utan female reproductive physiology in the wild remains a black box (for a review: Knott et al., 2009). Our behavioural data suggest that sexual interactions occur years prior to conception and therefore, likely during a period of lactational infertility. Previous studies have shown that male initiated sexual interactions occur largely decoupled from female ovarian state (Knott et al., 2010; Nadler, 1981). Also our preliminary data on female progesterone metabolite levels suggest that sexually attractive females have not necessarily resumed ovarian cycling activity. First, we found hardly evidence for elevated fPdG levels during periods when females were known to be sexually active, as would be expected during the luteal phase of cycling females (one exception). Also our permutation tests based on an ovulatory cycle profile from a captive female orang-utan indicate that the fPdG levels of sexually active females in the wild do not exhibit the expected variability of fPdG levels. However, our sample sizes per individual female are extremely limited, which does not allow for a closing statement. Although it seems unlikely, we may have simply not captured the luteal phase due to a sampling bias. In future studies, hormone levels from urine samples, which also contain oestrogen metabolites (which could not be detected reliably in orang-utan faeces, M.H., unpubl. data), may help to assess female reproductive physiology more conclusively. Previous studies have shown that female reproductive hormone levels are tightly linked to fruit availability and thus, known conceptions were clustered during such high food availability periods (Knott et al., 2009).

Evaluating the correlates of female reproductive physiology are crucial not only to understand male-female relationships and the underlying sexual conflict, but also for more applied conservation measures. Unfortunately, due to ethical considerations, logistic and administrative obstacles, the semi-solitary lifestyle (Rijksen, 1978; van Schaik, 1999) and the slow reproduction of orang-utans (van Noordwijk et al., 2018; Wich et al., 2009), it is difficult to obtain the necessary high resolution on female reproductive hormones in the wild, i.e. repeated urine or faecal samples over several weeks or months from the same individual at the period prior to conception. Hair samples may provide a viable alternative to assess female ovarian activity over several months in future studies (Carlitz et al., 2014). For now, we hypothesize that non-preferred male orang-utans, who do not receive female proceptive behaviour around ovulation, do not have reliable cues of the female (endocrine) reproductive state, as suggested by previous studies (Knott et al., 2010; Nadler, 1981). In any case, because the occurrence of ovulatory cycles is generally unpredictable in great apes (Deschner et al., 2004; Douglas et al., 2016; van Noordwijk and van Schaik, 2000), males may benefit from mating due to a small but non-zero chance of siring offspring.

Acknowledgements

We would like thank Adrian Baumeyer and Gabi Rindlisbacher from the Basel Zoo for collecting urine samples for our pilot study. Further, we are grateful to Gholib for his support during the hormone analyses.

Chapter 5: Context of Sexual Coercion

Occurrence of sexual interactions in dyadic associations

Female resistance was sometimes successful and the male stopped his copulation attempt (for details see chapter 4). Also when including these female-resisted failed attempts, the probability of female resistance was best explained by the age of her dependent infant, the male morph, the association duration and the occurrence of displacement events by another male (Stable 33).

Stable 33 Output of binomial GLMM on the occurrence of female resistance to male-initiated sexual interactions (including both copulations and failed attempts) within dyadic associations (N=960 of 174 male and 31 female identities) involving parous females only depending on ecological, physiological and immediate social factors. The comparison of the full model with the null model (random intercepts only) and the control model are reported below.

Fixed effects	**Estimate**	**SE**	**Odd's ratio**	**z value**	**P value**
Intercept	-2.659	0.381			
Site (Suaq vs. Tuanan)	-0.512	0.389	0.60	-1.318	0.188
z Age of dependent infant (y)	1.253	0.253	3.50	**4.959**	**<0.001**
Male morph (unflanged vs. flanged)	-1.962	0.414	0.14	**-4.735**	**<0.001**
z Fruit Availability Index	-0.041	0.151	0.96	-0.272	0.786
z Assocation duration	0.659	0.149	1.93	**4.414**	**<0.001**
z Overall total time spent in dyad (hours)	-0.079	0.158	0.92	-0.502	0.616
Number of other males in association with female that day	-0.176	0.164	0.84	-1.073	0.283
Displacement by another male	0.690	0.350	1.99	**1.969**	**0.049**
Displacing another male	0.634	0.396	1.89	1.602	0.109
$\chi^2_{4,12}$=111.09, P<0.0001, ΔAIC =93.09					
$\chi^2_{8,12}$=33.89, P<0.0001, ΔAIC =23.89					

Zero-inflated model

Because copulations rarely occurred during dyadic associations, our data may seem zero-inflated. Copulations during the focal follow are unlikely to be missed by observers, because they last for several minutes and involve two unrelated individuals in body contact, which rarely occurs during orang-utan associations. Yet, if associations last overnight, copulations may occur during the absence of observers. Therefore, our dataset might have some zero-inflation. For this reason, we conducted a GLMM accounting for zero-inflation to report that patterns still hold (Stable 34): Males who were displaced from proximity to females were still more likely to experience female resistance, even when accounting for possible zero-inflation. Yet, the probability that displacing males had non-resisted copulations did not show up anymore.

Stable 34 Output of a zero-inflated, binomial GLMM ('glmmTMB') on the occurrence of resisted (a) and non-resisted (b) copulations within dyadic associations (N=960 of 174 male and 31 female identities) involving parous females only depending on ecological, physiological and immediate social factors. The comparison of the full model with the null model (random intercepts only) and the control model are reported below each model output.

Response	Fixed effects	Estimate	SE	z value	P value
Resisted copulations	Intercept	-4.112	0.664	-	-
	Site (Suaq vs. Tuanan)	-0.140	0.617	-0.227	0.821
	z Age of dependent infant (y)	1.624	0.360	**4.510**	**<0.001**
	Male morph (unflanged vs. flanged)	-1.898	0.516	**-3.675**	**<0.001**
	z Fruit Availability Index	0.077	0.192	0.402	0.688
	z Association duration	**0.726**	0.192	**3.782**	**<0.001**
	z Overall total time spent in dyad (hours)	0.004	0.183	0.022	0.982
	Number of other males in association with female that day	-0.130	0.194	-0.666	0.505
	Displacement by another male	1.048	0.417	**2.510**	**0.012**
	Displacing another male	0.433	0.469	0.923	0.356
	$\chi^2_{4,13}$=95.34, P<0.00001, ΔAIC=77.34				
	$\chi^2_{8,13}$=23.515, P=0.0003, ΔAIC =13.51				
Non-resisted copulations	Intercept	-3.295	0.754	-	-
	Site (Suaq vs. Tuanan)	0.444	0.696	0.639	0.523
	z Age of dependent infant (y)	2.433	0.862	**2.824**	**0.005**
	Male morph (unflanged vs. flanged)	-2.582	0.932	**-2.769**	**0.006**
	z Fruit Availability Index	0.465	0.291	1.595	0.111
	z Association duration	1.396	0.458	**3.049**	**0.002**
	z Overall total time spent in dyad (hours)	-0.008	0.237	-0.033	0.974
	Number of other males in association with female that day	-0.757	0.536	-1.412	0.158
	Displacement by another male	-0.478	0.872	-0.548	0.584
	Displacing another male	1.481	1.034	1.432	0.152
	$\chi^2_{4,13}$=95.34, P<0.00001, ΔAIC =77.34				
	$\chi^2_{8,13}$=43.82, P<0.00001, ΔAIC =33.82				

Including data on both nulliparous and parous females

Stable 35 Output of the binomial GLMM for the occurrence of resisted (a) and non-resisted copulations (b) in dyadic associations by study site, female parity, male morph, zFAI, association duration, total dyadic association time, the number of males in association and displacement events (N=1478 dyadic associations of 66 female and 219 male IDs)

Response	Fixed effects	Estimate	SE	Odd's ratio	z value	P value
Resisted copulations	Intercept	-5.400	0.791		-	-
	Site (Suaq vs. Tuanan)	1.362	0.685	3.90	**1.989**	**0.047**
	Female parity	1.123	0.528	3.07	**2.127**	**0.033**
	Male morph (unflanged vs. flanged)	-1.815	0.408	0.16	**-4.447**	**<0.001**
	z Fruit Availability Index	0.153	0.155	1.17	0.988	0.323
	z Association duration	0.884	0.151	2.42	**5.868**	**<0.001**
	z Overall total time spent in dyad (hours)	0.042	0.129	1.04	0.329	0.742
	Number of other males in association with female	0.115	0.158	1.12	0.726	0.468
	Displacement by another male	0.833	0.350	2.30	**2.383**	**0.017**
	Displacing another male	0.173	0.401	1.19	0.431	0.667
	$\chi^2_{3,12}$ =109.49, P<0.00001, ΔAIC=91.49					
Non-resisted copulations	Intercept	-3.628	0.501		-	-
	Site (Suaq vs. Tuanan)	0.644	0.459	1.900	1.404	0.160
	Female parity	-0.084	0.363	0.920	-0.232	0.817
	Male morph (unflanged vs. flanged)	-1.173	0.348	0.310	**-3.370**	**0.001**
	z Fruit Availability Index	0.083	0.127	1.090	0.656	0.512
	z Association duration	1.162	0.141	3.200	**8.249**	**< 0.001**
	z Overall total time spent in dyad (hours)	0.139	0.107	1.150	1.298	0.194
	Number of other males in association with female	0.083	0.149	1.090	0.553	0.580
	Displacement by another male	0.254	0.350	1.290	0.727	0.468
	Displacing another male	0.698	0.349	2.010	**1.998**	**0.046**
	$\chi^2_{3,12}$ =156.12, P<0.00001, ΔAIC=138.13					

Context of sexual interactions and female resistance

Stable 36 Probability of new male arrival within 1 hour after the last sexual interaction: Binomial GLM output of the probability that a new male arrived within 1 hour after the last observed sexual interaction of an association dyad (χ^2_5 = 15.77, P=0.008, ΔAIC=5.77, N=187 last copulations (of 28 female and 78 male IDs, which could not be accounted for in the analysis due to sample size issues)

	Estimate	SE	Odd's ratio	z value	P value
Intercept	-3.894	1.023			
Site (Suaq vs. Tuanan)	0.228	0.510	1.26	0.446	0.656
Female behaviour (non-resisted vs. resisted)	1.528	0.636	4.61	**2.401**	**0.016**
Parity (nulliparous vs. parous)	1.066	0.816	2.90	1.307	0.191
Male morph (unflanged vs. flanged)	-1.245	1.072	0.29	-1.162	0.245
zFAI	0.245	0.247	1.28	0.991	0.322

Stable 37 Latency to male arrival after sexual interaction: LMM output for the delay to the arrival of a new male associate (in minutes and square root-transformed) after a sexual interaction, given that there was a new male coming into association on the same day, depending on the site, female resistance behaviour (no/yes), the interaction between the two, female parity and male morph ($\chi^2_{4,9}$=16.14, P=0.006, ΔAIC=6.14; N=108 of 21 female IDs and 53 male IDs (included as random intercepts)).

	Estimate	SE	t value	P value
Intercept	11.267	2.343		
Site (Suaq vs. Tuanan)	2.676	2.081	1.286	0.223
Female behaviour (non-resisted vs. resisted)	-3.768	1.447	**-2.604**	**0.011**
Morph of arriving male (unflanged vs. flanged)	-0.593	1.224	-0.484	0.629
Parity (nulliparous vs. parous)	-2.554	1.833	-1.393	0.175
zFAI	-0.042	0.649	-0.065	0.949

Stable 38 Association maintenance after the last sexual interaction: Output of the survival analysis (using the 'coxme' package) for the probability that an association will be ended after the last sexual interaction depending on the site, female resistance, female parity and male morph. Female and male identity was added as a random intercept (χ^2_5= 8.76, P=0.12, N=162 ended associations (and a total of 258 last sexual interactions) of 34 female IDs and 86 male IDs).

	β	SE	Hazard ratio	z value	P value
Site (Suaq vs. Tuanan)	0.303	0.233	1.35	1.300	0.190
Female behaviour (non-resisted vs. resisted)	0.447	0.191	1.56	**2.340**	**0.019**
Parity (nulliparous vs. parous)	0.130	0.221	1.14	0.590	0.560
Male morph (unflanged vs. flanged)	-0.303	0.229	0.74	-1.320	0.190
zFAI	0.035	0.079	1.04	0.450	0.650

Analysis with subset of parous females only

Stable 39 Probability of female resistance behaviour: Binomial GLMM output on the probability of female resistance behaviour in a given dyadic sexual interaction depending on site, the age of the dependent offspring of parous females, the interaction partner's morph, the presence of either an additional unflanged or flanged male, and zFAI ($\chi^2_{3,9}$= 19.91, P=0.003, ΔAIC=7.91, N=226 copulations of 15 parous female IDs and 62 male IDs)

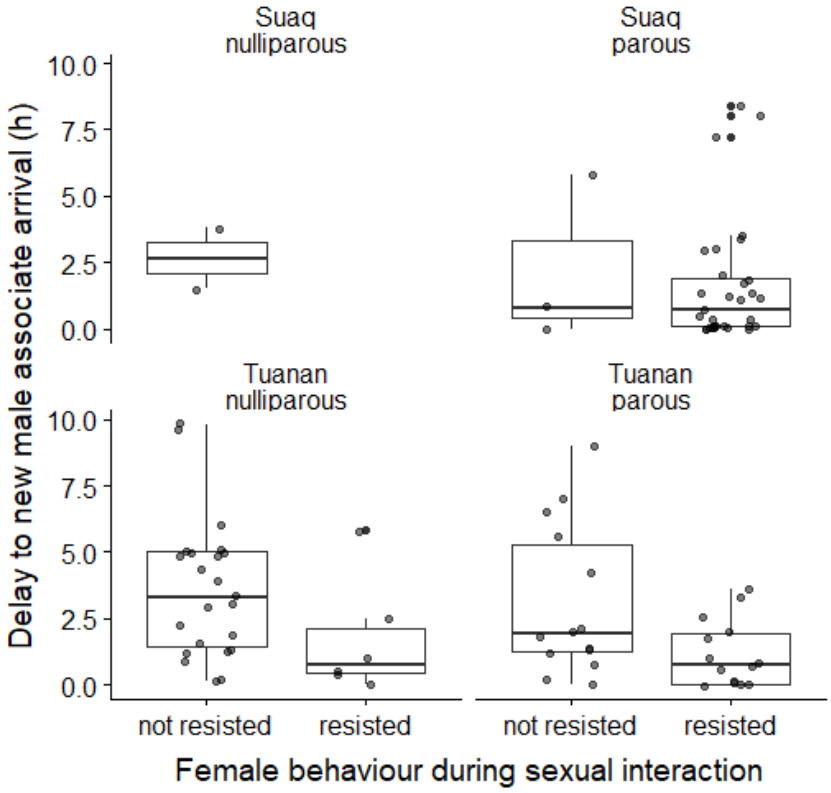
	Estimate	SE	Odd's ratio	z value	P value
Intercept	2.207	1.396			
Site (Suaq vs. Tuanan)	-0.770	1.308	0.46	-0.589	0.556
Age of dependent offspring (y)	-0.168	0.185	0.85	-0.908	0.364
Partner morph (unflanged vs. flanged)	-2.218	0.781	0.11	**-2.839**	**0.005**
Additional unflanged male present (no vs. yes)	0.695	0.562	2.00	1.236	0.217
Additional flanged male present (no vs. yes)	2.920	1.379	18.54	**2.117**	**0.034**
zFAI	0.209	0.253	1.23	0.825	0.409

Stable 40 Latency to the arrival of a new male (min): LMM output for the latency (min) to the arrival of a new male after a sexual interaction involving parous females only ($\chi^2_{3,6}$=5.10, P=0.16, ΔAIC=0.90; N=62 [of 12 female IDs] and 35 male IDs).

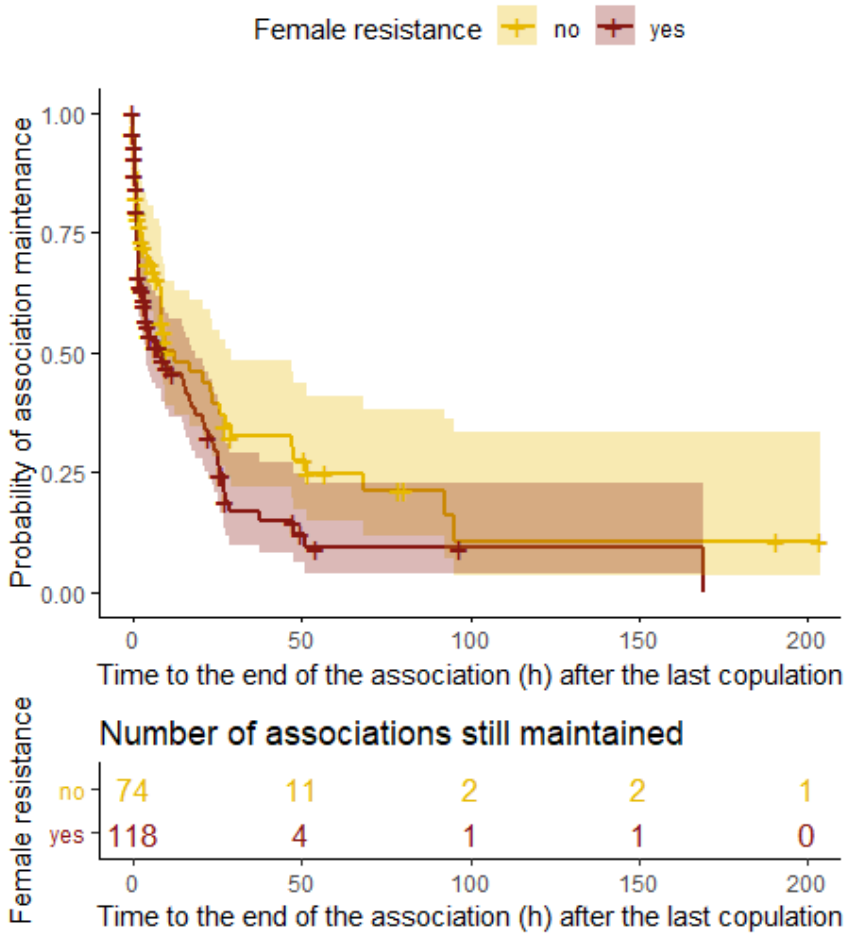
	Estimate	SE	t value	P value
Intercept	11.169	2.223		
Site (Suaq vs. Tuanan)	0.522	1.995	0.262	0.795
Female behaviour (non-resisted vs. resisted)	-3.957	2.030	-1.949	0.056
Morph of arriving male (unflanged vs. flanged)	-0.569	1.757	-0.324	0.747

Stable 41 Association maintenance after the last sexual interaction in a given association dyad: Output of the Cox proportional Hazard model (survival analysis) for the probability that an association will be maintained after the last sexual interaction depending on the site, female resistance, and male morph. Female identity was added as a random intercept (χ^2_4=6.82, P=0.15, N=124 ended associations [and a total of 191 last sexual interactions] of 23 parous female IDs and 74 male IDs).

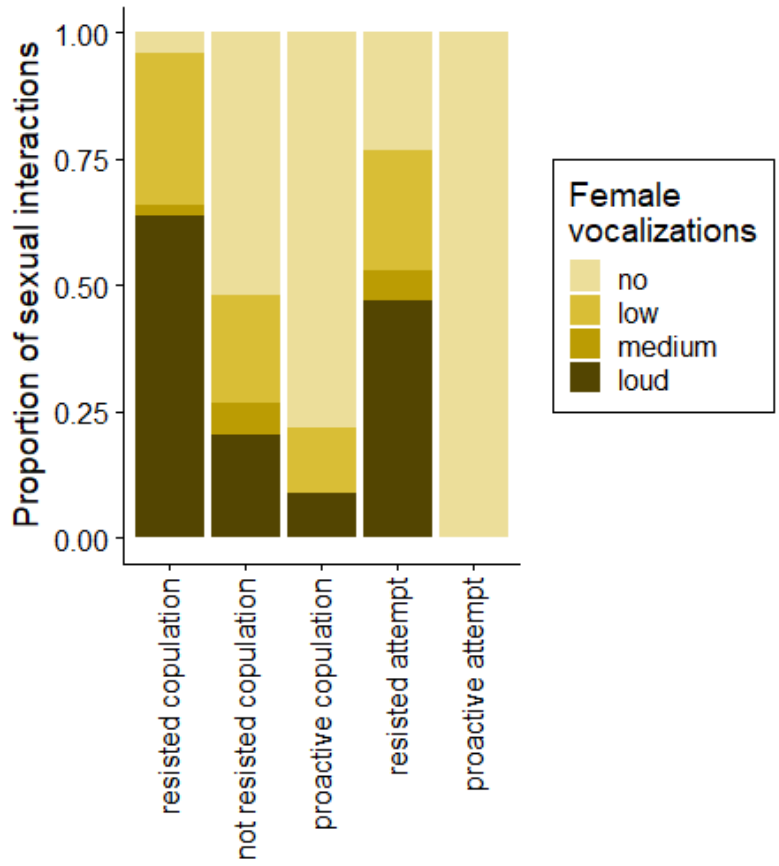
	β	SE	Hazard ratio	z value	P value
Site (Suaq vs. Tuanan)	0.361	0.257	1.435	1.400	0.160
Female behaviour (non-resisted vs. resisted)	0.476	0.226	1.610	**2.100**	**0.035**
Male morph (unflanged vs. flanged)	-0.233	0.259	0.792	-0.900	0.370
zFAI	0.056	0.106	1.057	0.520	0.600



Sfigure 19 Latency to the arrival of new male associates depending on the occurrence of female resistance during sexual interactions by site (*top:* Suaq; *bottom:* Tuanan) and female parity (*left:* nulliparous; *right:* parous)



Sfigure 20 Kaplan-Meier survival curves for the probability of association maintenance after sexual interactions depending on the occurrence of female resistance. The delay to the end of the association (x-axis) after the last sexual interaction of dyadic associations involving only parous females are included in this figure. Below the survival curve plot on the probability of association maintenance the table including the number of associations that were still maintained is given.



Sfigure 21 Female vocalization proportion during sexual interactions by the type of sexual interaction and the vocalization intensity (colours)

Discussion

Variation between study sites

We could not find any evidence for study site differences concerning copulation occurrence during dyadic association or its immediate context. Nonetheless, the pattern of an earlier male arrival after a female-resisted sexual interaction tended to be more pronounced at Tuanan than Suaq. This trend fits with previous findings on male morph specific study site differences. First, copulation rates based on female follow data tend to be higher at Suaq than at Tuanan (chapter 4), which then is the direct result of the overall higher association frequency at Suaq and not due to higher interaction rates *per se* (chapter 3; Mitra Setia et al., 2009; van Schaik, 1999). Second, unflanged males at Suaq were more likely to experience female resistance, than at Tuanan (chapter 2). In the light of our suggested *"not-you-now"* hypothesis, both higher copulation and coercion rates at Suaq are expected, because of the high population density and extraordinary sociability (Mitra Setia et al., 2009; van Schaik, 1999) with (unflanged) males forming temporary travel bands (Reukauf, 2019; van Schaik, 1999). Thus, males are more likely to be simultaneously in association with females and hence, male competition may be incited, although this rarely manifests in overt male-male aggression (Reukauf, 2019; Utami Atmoko et al., 2009b) but in increased mating rates. Furthermore, subordinate males at Suaq are less constrained by ecological costs to remain in vicinity to females after a displacement event (Mitra Setia et al., 2009; van Schaik, 1999) and follow the male-female dyad counting on a sneak copulation opportunity (Fox, 2002; Utami Atmoko et al., 2009a). With the data presented here, we cannot infer, if the female resisted copulation happened prior or past a certain displacement event, because our definition ("the displacement from the proximity of a female"; Tab.1) did not necessarily imply the immediate end of an association. The absence of site differences may therefore arise from this imprecision in our current

analyses. We hypothesize that in less sociable populations, such as Tuanan's, displacement events lead more likely to the end of an association than in more sociable populations, such as Suaq's, because of the higher costs of association and reduced tolerance among (unflanged) males (Galdikas, 1985b).

The link between male competition and female resistance also offers an explanation for our previous findings that individual flanged males' coercion frequency does not differ between Suaq and Tuanan (chapter 2). Although there is more direct contest competition among flanged males in Tuanan than Suaq (Dunkel et al., 2013; Spillmann et al., 2017; Utami Atmoko et al., 2009b), flanged males are generally dominant over unflanged males, avoid associations and direct confrontation in physical fights with other flanged males (Mitani, 1985b; Rijksen, 1978; Spillmann et al., 2017; Utami Atmoko et al., 2009b) and are more selective with which females to associate and copulate (chapter 2; MacKinnon, 1974; Schürmann, 1982; Utami Atmoko et al., 2009a). Hence, it may be extremely rare that flanged males are at the risk of displacement and thus, hardly resume to force copulations, but also hardly experience female resistance. Rather flanged males are the males who displace other (unflanged) males and accordingly, are more likely to have non-resisted copulations. Knott and colleagues (2010) suggested that past-prime flanged males experience more female resistance at Gunung Palung (West Kalimantan). With their lower fighting abilities, the risk of displacement was likely high. At Tuanan, both confrontational assessment in long call exchanges (Spillmann et al., 2017) and physical fights among flanged males are more likely around sexually active females (Spillmann, 2017; review on different sites: Utami Atmoko et al., 2009b). Thus, direct contest competition and aggression among flanged males is also directly linked to mating access and female preference for dominant males.

Taken together, especially in populations with unstable male dominance relationships, as reported mostly for Bornean populations (Delgado and van Schaik, 2000; Dunkel et al., 2013; Spillmann et al., 2017), being dominant or subordinate may be highly context dependent, and thus, male and female tactics change variably with the presence of other males. This is further supported by the occurrence of the coercive hand-holding at Tuanan, but not at Suaq (Russon et al., 2009; van Schaik et al., 2006). Even flanged males (and dominant unflanged males) were observed to reside to such mate guarding techniques if potential competitors were around. When male dominance relationships are stable, dominant flanged males in (West) Sumatran populations can rely on female preferences (Fox, 2002, 1998; Mitra Setia and van Schaik, 2007). In populations like Tuanan, with unstable male dominance relationships leading to high levels of confrontational assessment among flanged males (Dunkel et al., 2013; Spillmann et al., 2017), they cannot always rely on female choice and thereby sexual conflict among flanged males and females may be more likely to arise.